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Nectar, Humidity, Honey bees (*Apis mellifera*) and Varroa in summer: A theoretical thermofluid analysis of the fate of water vapour from honey ripening and its implications on the control of *Varroa destructor*.

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Abstract

This theoretical thermofluid analysis investigates the relationships between: honey production rate, nectar concentration, and the parameters of: entrance size, nest thermal conductance, brood nest humidity and the temperatures needed for nectar to honey conversion. It quantifies and shows that nest humidity is positively related to the amount, and water content of the nectar being desiccated into honey and negatively with respect to nest thermal conductance and entrance size. It is highly likely that honey bees, in temperate climates and in their natural home, with much smaller thermal conductance and entrance, can achieve higher humidities more easily and more frequently than in man-made hives. As a consequence it is possible that *Varroa destructor*, a parasite implicated in the spread of pathogenic viruses and colony collapse, which loses fecundity at absolute humidities of 4.3 kPa (~30 gm^{-3}) and above, is impacted by the more frequent occurrence of higher humidities in these low conductance, small entrance nests. This study provides the theoretical basis for new avenues of research into the control of varroa, via the modification of bee keeping practices to help maintain higher hive humidities.

1 Introduction

The phenotype, the physical reflection of the gene, cannot be limited to purely the biological aspects of the organism itself because it directly causes change to the environment around it [1], in accordance with the laws of thermodynamics and mass and energy conservation. For most organisms the realm of their influence extends only a very small distance from the biological tissue of the animal. However for those in which this goes beyond the usual, and their reach into environment is significant, then it is termed an “extended phenotype”. The classic case cited is of beavers flooding areas with their dams [2]. For honey bee colonies, perhaps because of the relationship with man the extended nature of this super organism’s [3] phenotype has been overlooked, and viewed as a simple shelter and container of honey and brood. In contrast to the beaver’s dam, which constrains a single visible fluid, some of the fluids involved in a honey bee colony’s nest: air, water vapour, water liquid and carbon dioxide are invisible to human eyes. These fluids are not passively restrained, but actively moved and changed in temperature and physical state within this extended phenotype. In addition: heat flux through the nest walls and entrance [4]; condensation and evaporation of water; and desiccation of nectar into honey, literally sugar refining, some of which is metabolised/“burnt” [5]. Thermofluids is defined as the study of fluid flows, heat transfer including phase changes and the combustion of fluids [6]. Therefore comprehensive analytical study of a honey bee’s extended phenotype must include analysis based on thermofluids and apply its relevant tools. That these are more commonly used to analyse sugar refineries, buildings or nuclear power plants should not be seen as a barrier [1].

Research into honey bees is almost exclusively executed in man-made hives, and with only two exceptions [4,7], without any measurement of the hives physical characteristics. Unsurprisingly, there is very little quantitative research or analysis [4,8] into their thermofluid properties. It is from this low level that this analysis endeavours to understand the interplay of some of the thermofluid processes.

It is important to note that in this document the unqualified term, humidity, will be only used to refer to the absolute humidity expressed as the vapour pressure in kPa or as a tuple of the saturation ratio χ, and the absolute temperature T denoted as $\{\chi, T\}$. Thus the humidity of 80% saturation at 34 °C is shown as 4.3 kPa and/or {0.8, 307.2 K} from equation (3.1). The saturation ratio, (relative humidity), will be clearly denoted if used. The dew point temperature is the temperature T_D, for that humidity, where the air is at complete saturation i.e. $\{1.0, T_D\}$. Thus, because {0.8, 307.2 K} equals 4.3 kPa which equals {1.0, 303.2 K}, then one can say the dew point temperature of {0.8, 307.2 K} is 303.2 K.

Honey, a high sugar concentration (>0.8) fluid, is made by honey bees from flower nectar, a lower sugar concentration liquid (0.1 - 0.5), collected from numerous flowers sometimes at considerable distance from the nest (up to 9 km) [9]. This nectar is passed by the forager honey bee to another [10] honey bee (unloader /storer), which then starts the desiccation process by selectively heating and aerating the nectar with their mouth parts, while placing it in a honey comb cell. This partially desiccated nectar is then exposed to low humidity air [11], while the hive population engages in vigorous forced air movement within the nest by fanning their wings [10,12,13]. This very energy intensive [8] process of nectar to honey conversion is placed above the brood nest in order to have less than 0.62 relative humidity (RH). After the desiccation process is completed, the cell may be capped with wax to prevent the reabsorption of water vapour. This RH value χ_{Honey}, when honey is in equilibrium with the vapour in the air, is termed the water activity of honey [11]. It has been shown to range from 0.5 to 0.7 and has a linear relationship with the water content of the honey, equation(1.1) [14] (See table 1 for term definitions and values).

$$\chi_{Honey}=0.2686+1.756\left(1-C_{Honey}\right) \tag{1.1}$$

There are differences between subspecies as to when they begin the desiccation process, *A. m. scutellata* in dry hot climates, has been observed to reduce the water content by 50% in flight [15], where as *A.m. mellifera* and *A.m ligustica* in cooler climates do not [10].

In a nest with a single opening, all fluids from nectar desiccation and other processes must permeate through the walls or pass through the entrance. Water vapour and carbon dioxide can be removed by honey bees fanning at the entrance [5], achieving a maximum entrance air velocity of approximately $1ms^{-1}$ [16,17]. While bee keepers often, in addition to a mesh floor, provision multiple entrances in summer totalling over 80 cm^2 [18]; honey bee swarms prefer nests with single entrances of $12cm^2$ or smaller[5]. However, water vapour converts back to a liquid by condensation, a process which needs energy to be removed from the water vapour laden air. The principle of conservation of energy means that the rate of condensation is dependant on the lumped conductance of the nest walls, and the temperature difference between the dew point temperature of the humidity on the inside surface in the condensing zones and the outside air.

Values for the nest lumped conductance in a winter configuration have been experimentally measured [4] and represent a realistic estimate of the lower end of nest conductance. A realistic upper limit for nest conductance can be found analytically using standard shape factors [19].

The permeability of the honey bee applied propolis lining (plant resins) is of the order of 10^{-13} $kgm^{-1}s^{-1}Pa^{-1}$ [20]. This results in a flow rate of the order of 2 mgs^{-1} at a water vapour pressure differential of 5 kPa and thickness of 0.25 mm. This is insignificant compared to water removal rates up to 100 mgs^{-1} for condensation and advection.

Research into the humidity relations of *A.mellifera,* while less extensive than for temperature, has found that honey bee eggs require 5.1 kPa {0.9, 308.2K} for development [21] and larvae require greater than 4.1kPa {0.75, 307.7 K} [22]. The particularly high humidity for honey bee egg hatching should be taken in context that the eggs are laid at the far end of the cells, a microclimate separated from the general nest environment [23,24]. However fully grown larvae, which may then be infested with varroa, have conditions approaching that of the general nest environment.

Researchers have shown varroa fecundity falls significantly at humidities close to 4.3 kPa i.e. [25] 4.3 kPa {0.8 307.2 K}, [26] 4.2 kPa {0.75, 308.2 K}, [27] 4.3 kPa {0.7, 309.7 K}, [28] 4.2 kPa {0.872, 305.6 K}. Despite this, varroa has spread to honey bee colonies in a wide range of climates.

Condensate collection inside the hive or water disposal in the liquid phase by *A.mellifera a*re not addressed in the literature. This absence has been noted by others [29].

The most recent and comprehensive studies into honey bee nest humidity have been undertaken by the Zoology department of the University of Pretoria in South Africa (ZDUPSA), and in a body of work related to humidity for *A.m. scutellata* have covered: the effects of external weather, winter clustering, differing nest types, hygropreference and honey bee fanning behaviour [15,30–33]. This analysis, inspired by their work, seeks to provide the thermofluid theory to both explain and extend it, while using their climate and fanning data for input, and their results for experimental validation where possible.

2 Approach

This analysis will use a steady state, simple zoned temperature model of the nest cavity with a single bottom entrance, all at the same constant humidity, but at different average temperatures and consequently different average relative humidities consisting of :

- A honey/nectar zone below 0.6 RH at a temperature above 307.7 K [14,30].
- A brood zone at 307.7 K (34.5 °C) with a maximum humidity of 4.9 kPa {0.9, 307.7 K} [5,30].
- A condensing zone at the dew point temperature I.e. internal surface of the cavity.

In this model, which is a simplification of a complex system:

- Water vapour enters the system from nectar evaporation, nectar consumption and through entrance inlet air flow by forced convection.
- Water vapour leaves via condensation and entrance exhaust flow.
- Heat energy is produced by metabolising sugars.
- Heat energy exits via conduction through the nest walls. The heat flows of the entrance gases are insignificant in comparison (~10mW vs ~100W) [8] and ignored.
- The pollen to insect protein processes are considered as a constant rate metabolic energy overhead that consumes nectar, releasing water vapour from its water content and oxidation.

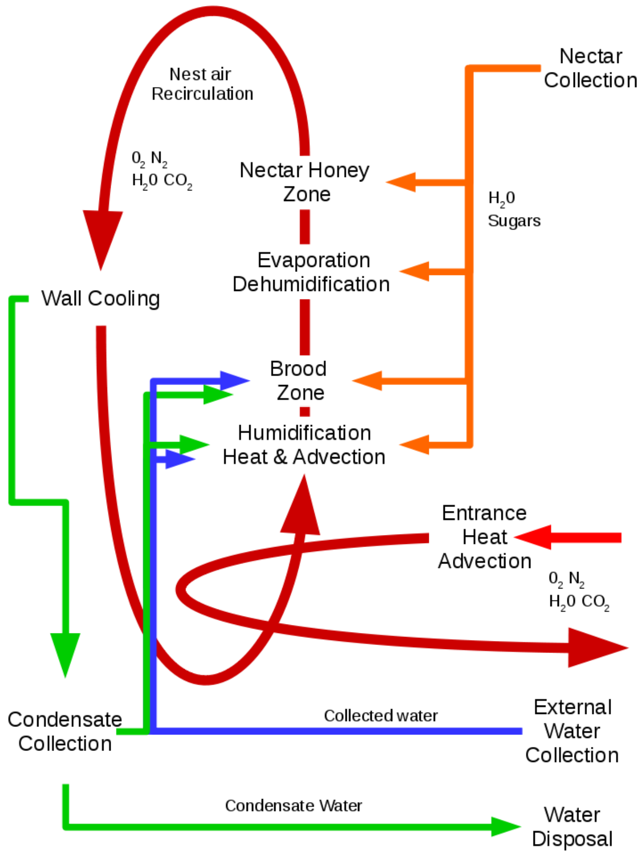

Figure 1: Nest fluid transfer and phase change processes

In reality the honey bee nest is a set of complex interconnected processes as shown in Figure 1, involving the fluids: nectar (orange), externally collected water (blue), condensate water (green), and gases (red). The latter are a mixture of air, water vapour and CO_2. These are advected through the entrance and circulated between: a brood zone kept at constant temperature, a nectar zone at elevated temperature for evaporation, and a lower temperature condensation zone.

By using the standard thermofluid techniques of energy and mass balances across the system boundary to determine the ability of honey bees to dispose of the water vapour generated and therefore the resultant average humidity, this approach removes the necessity to analyse the internal detail while retaining validity.

To populate the model, the climatic and fanning behavioural data are from ZDUPSA [30] and the results, generated using MATLAB [34] are correlated to their findings [31–33].

2.1 Water vapour production rate

For the purposes of this analysis, water vapour production consists of 5 components:

- Water evaporated from nectar, at honey production rates of 5 mgs^{-1} (1 lb/day) and may exceed 25 mgs^{-1} (5lb/day) [10,12].
- Water content from the nectar used as fuel for nectar evaporation.
- Metabolic water production from the nectar used as fuel for nectar evaporation.
- Water content from the nectar used for other processes in the nest.
- Metabolic water production from the nectar used for other processes in the nest.

The weight of water entering the vapour phase in the nest is defined in equation.

$$\dot{W}_{Vapour}^{Total}=\alpha\dot{W}_{Water}^{Evaporate}+[\dot{W}_{Nectar}^{Nest}+\dot{W}_{Nectar}^{Evaporate}][\beta_0(1-C_{Nectar})+\beta_1 C_{Nectar} r] \quad (2.1)$$

The coefficients α β_0 β_1 defines the proportion resulting in water vapour (vapour fraction) inside the nest from 3 classes of water source:

- Water content of nectar that is "made" into honey α .
- Water content of the nectar consumed as metabolic fuel β_0 .
- Water from the oxidation of the sugars from nectar consumed as fuel β_1 .

Similarly, $1-\alpha$ $1-\beta_0$ and $1-\beta_1$ are the proportions that are excreted or do not arrive at the nest.

If one considers only the delivered nectar concentration, as opposed to the collected nectar concentration, then differences between races of honey bee desiccating the nectar in flight can be ignored (*A.m. mellifera and A.m. ligustica* [35] versus *A.m. scutellata* [15]). Then according to the behaviours described one may determine $\alpha\approx 1$ [35]. From the winter behaviour of not defecating for extended periods [5], one can deduce that β_1 can be close to unity and, from their consumption of honey with a ~0.2 water content during winter, that β_0 can be non zero. More precise values, or the validity in the nectar gathering season, are unknown. The analysis can assess the significance of these coefficients and consequently their importance for further research. For other purposes, assumptions may have to be made about these coefficients.

The amount of water to evaporate and the fuel required for evaporation $\dot{W}_{Water}^{Evaporate},\dot{W}_{Nectar}^{Evaporate}$ are dependent on rate of honey production, nectar concentration and the thermal efficiency of the nectar evaporating process TEE or $\Gamma_{Thermal}$, as shown in the expressions in previous work [8]. TEE is derived from the nest thermal conductance. However, depending on the nest configuration and the honey bee behaviours, the nest thermal conductances for evaporation and condensation may differ from each other, particularly in larger or higher aspect ratio nests that may give more space for stratification. Using the equation for the break-even energy margin from [8], an equation can be derived that gives maximum water vapour production at the minimum thermal efficiency for a specific nectar and honey concentration.

The rate of consumption of nectar for other metabolic processes $\dot{W}_{Nectar}^{Nest}$ is dependant on the honey bee colony mass and the metabolic rate, which is dependant on the nest internal temperature and hence the external temperature and the nest thermal conductance [4]. However, as a simplification this rate of consumption will be assumed to be disjoint from the evaporation and condensation processes and a fixed value in this analysis, to concentrate on the effects of nectar condensation. Full integration into the analysis is left for future research.

2.2 Water removal rate

The total capacity for water removal is the sum of the water vapour that exits the entrance and that condensed inside the nest. The rate of condensation is defined by the latent heat lost through the nest walls as heat lost via entrance air flow is insignificant in comparison. The water vapour exhausted is characterised by the vapour density of the air and the total flow through the entrance. The maximum dew-point temperature and hence exhaust water vapour density and exhaust water mass are defined by the following constraints:

1. The brood area is not above 4.9 kPa {0.9, 307.7K} [30]. This defines the limit of the vapour pressure and vapour density for the gas exhausted by fanning and the dew point for condensation.
2. Honey can be ripened. This defines a vapour pressure that results in the maximum honey water activity (0.6) below a maximum achievable honey bee temperature of 318.2 K [36].
3. The maximum fanning air velocity (0.924 ms^{-1} [17])

The fanning response to humidity is fitted, using a cubic polynomial (R-square 0.9934), to the ZDUPSA normalised data with the presence of brood [30], as shown in figure 2, assuming the honey bees deliver air velocity proportional to this response up to their maximum.

Fanning responses to carbon dioxide levels can be ignored as they cannot exceed 20% of water vapour partial pressure during nectar evaporation [8,37].

The climatic information i.e. ambient temperature and humidity used in analysis will be for the same location i.e. Pretoria South Africa averages for spring and summer (November to February) of 295.7K (22.5C) and 0.595 RH [38].

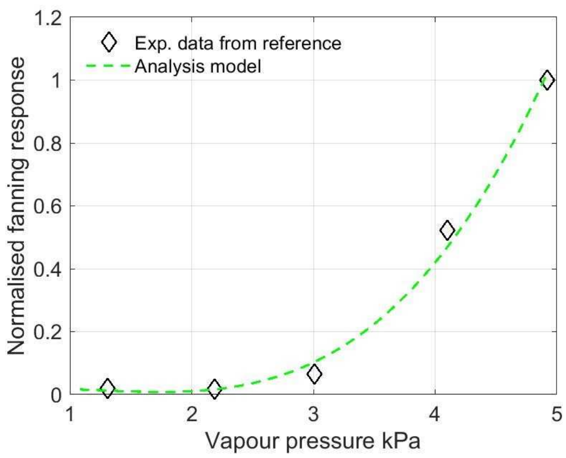

Figure 2: Fanning response versus vapour pressure kPa using data from [30]

Honey bee constructions and behaviours, as well as the nest walls, define a lumped conductance for the condensation process. Limits of conductance of the nest walls for both tree and man-made nests are derived from standard shape factors and techniques [19] using average dimensions from the literature [4,39]. For hives, the upper limit of one brood box and 4 shallows [18] will be used.

The energy balance of wall heat conduction and the heat produced by condensation, produces an equation in terms of the dew point, which is then solved.

Term	Value	Description	Units
A		Factor of coefficient α – vapour fraction of water content of nectar made into honey	-
B_0		Factor of coefficient β_0 - vapour fraction of water content of nectar used as fuel for nectar evaporation	-
B_1		Factor of coefficient β_1 - vapour fraction of water from oxidation of nectar used as fuel for nectar evaporation	-
$A_{Entrance}$		Cross sectional area of entrance	m^2
C_{Nectar}		Concentration of Nectar	$kgkg^{-1}$
C_{Honey}	0.8	Typical concentration of sugars in honey [5]	$kgkg^{-1}$
d_0	0.2	Diameter of tree cavity [39]	*m*
d_1	0.5	External diameter of tree [39]	*m*
$\dot{L}_{meta}$	10	Background colony metabolic rate [40]	Wkg^{-1}
h_{Tree}	1.4	Height of tree cavity [39]	*m*
h_{Hive}	0.825	Internal vertical dimension of hive with 4 shallows and one deep.[18]	*m*
$L_{Sucrose}$	15.1	Latent heat of combustion of sucrose (lower heating value, water remains vapour).[41]	$MJkg^{-1}$
L_{Water}	2.43	Latent heat of water vapourisation at 305K (32.8C).[42]	$MJkg^{-1}$
r	58	Weight of metabolic water released per kilo of sucrose metabolised.	$kgkg^{-1}$
T_{Brood}	307.66	Brood temperature [30]	*K*
T_D		Dew point temperature	*K*
T_i		Temperature instance i	*K*
T_{Out}	295.66	Temperature Outside – For ZDUPSA Average Pretoria spring summer (November – February) temperatures [38]	*K*
u_{Ent}		Air velocity through entrance	ms^{-1}
u_{EntMax}	0.94	Maximum entrance air velocity [17]due to fanning	ms^{-1}
$W_{Sucrose}^{Base}$		Weight of sucrose in resultant honey	kg
W_{Colony}	2	Background colony population those not involved in foraging or evaporations~20,000 honey bees [5]	kg
$W_{Nectar}^{Delivered}$		Weight of nectar delivered to nest	kg
$W_{Nectar}^{Evaporate}$		Weight of nectar required as fuel for the evaporation of nectar	kg
$\dot{W}_{Water}^{Evaporate}$		Rate of water evaporated in honey ripening	kgs^{-1}
$\dot{W}_{Nest}^{Nectar}$		Rate of nectar consumption from other processes than honey evaporation	kgs^{-1}
$\dot{W}_{Honey}^{Base}$		Rate of honey ripening in terms of resultant honey	kgs^{-1}
$\dot{W}_{Vapour}^{Total}$		Rate of water vapour production from all sources inside the nest	kgs^{-1}
$\hat{\dot{W}}_{Vapour}^{Total}$		Rate of water vapour removal by all methods inside the nest	kgs^{-1}
x_0	0.440	Internal horizontal dimension of hive [18]	*m*

Term	Value	Description	Units
x_1	0.478	External horizontal dimension of hive [18]	*m*
α	1	Proportion of evaporate water emitted as vapour while in the nest	-
β_0	1	Proportion of water content of nectar consumed emitted as vapour while in the nest	-
β_1	1	Proportion of sugar content of nectar consumed emitted as vapour while in the nest	-
$\Gamma_{Thermal}$		TEE Thermal efficiency of desiccation	-
ξ		Reciprocal concentration of honey subtract from reciprocal concentration of nectar	-
ρ_i		Density of Water Vapour in instance i	kgm^{-3}
ρ_{Inlet}		Density of Water Vapour entering entrance	kgm^{-3}
$\rho_{Exhaust}$		Density of Water Vapour exiting entrance	kgm^{-3}
Λ_{Evap}		Thermal conductance of the nest enclosure e.g. hive, tree etc. for evaporation processes	WK^{-1}
Λ_{Con}		Thermal conductance of the nest enclosure e.g. hive, tree etc..for condensation processes	WK^{-1}
λ_{Tree}	0.2	Thermal conductivity of tree wood [4]	$Wm^{-1}K^{-1}$
λ_{Hive}	0.12	Thermal conductivity of hive wood [4]	$Wm^{-1}K^{-1}$
χ_i		Relative humidity instance i	-
χ_{Brood}		Relative humidity inside the brood zone	-
χ_{Out}	0.6	Outside relative humidity For ZDUPSA Pretoria summer spring relative humidity [38]	-
χ_{Honey}		Typical water activity of honey i.e. RH	-
θ_i		Water vapour pressure derived parameter	*Pa*
γ_i		RH derived dimensionless parameter	-
δ_i		Temperature derived dimensionless parameter	-

Table 1: Nomenclature

3 Analysis

3.1 Assumptions

The following assumptions in addition to those in section 2 are made:

1. System is in equilibrium i.e. steady state.
2. Entrance air velocity is proportional to fanning response and is independent of entrance size i.e. sufficient fanning honey bees will be recruited.
3. Water vapour losses or gains through permeation of the nest enclosure and its internal coating of propolis are insignificant.
4. Water vapour pressure is the same throughout the nest or hive.
5. There is only one entrance or vent and it is at the bottom of the nest or hive.
6. The energy changes due the thermal capacities of the fluids crossing the system boundaries are negligible compared to those involved in the state changes.

3.2 Basics

The partial pressure of water vapour is given in equation (3.1) after [43,44]

$$P_i = 610.78\,\chi_i\, e^{\left[17.2694\frac{T_i - 273.16}{T_i - 35.86}\right]} \tag{3.1}$$

and the vapour density from (3.2).

$$\rho_i = 0.002166\,\frac{P_i}{T_i} \tag{3.2}$$

Let the following parameters be defined for instance *i* of temperature, relative humidity and vapour pressure in (3.3), then equation (3.1) becomes (3.4) and at the dew point (3.5)

$$\delta_i = \frac{T_i - 273.16}{T_i - 35.86} \qquad \gamma_i = \frac{\log \chi_i}{17.2694} \qquad \theta_i = \frac{1}{17.2694}\log\left(\frac{P_i}{610.78}\right) \tag{3.3}$$

$$\theta_i = \gamma_i + \delta_i \tag{3.4}$$

$$\theta_D = \delta_D \tag{3.5}$$

If conditions change (RH, temperature) but the vapour pressure remains constant from instance *j* to *i* then equation (3.6).

$$\theta_j = \theta_i = \gamma_j + \delta_j = \gamma_i + \delta_i \tag{3.6}$$

Then (3.7), (3.8) and (3.9)

$$P_i = 610.78\,\mathrm{e}^{[17.2694\,\theta_i]} \tag{3.7}$$

$$T_i = \frac{273.16 - 35.86\,\delta_i}{1 - \delta_i} = \frac{273.16 - 35.86\,(\theta_j - \gamma_i)}{1 - (\theta_j - \gamma_i)} \tag{3.8}$$

$$\chi_i = \mathrm{e}^{[17.2694\,\gamma_i]} = \mathrm{e}^{[17.2694(\theta_j - \delta_i)]} \tag{3.9}$$

The upper limits of conductance for condensation in tree nests and man-made hives are derived from the conductance being the sum of the products of conductivities and shape factors of the components forming the cavities. For the tree nest equation (3.10)

$$\Lambda_{Con} \approx \lambda_{Tree} \left[\frac{2\pi h_{Tree}}{\ln\left(\frac{d_1}{d_0}\right)} + 2\frac{\pi d_0^2}{4} \frac{1}{\frac{1}{2}(d_1 - d_0)} \right] \tag{3.10}$$

For man-made hives with roof thickness identical to the walls (3.11)

$$\Lambda_{Con} \approx \lambda_{Hive} \left[\frac{2\pi h_{hive}}{0.785 \ln\left(\frac{x_1}{x_0}\right)} + 2\frac{x_0^2}{\frac{1}{2}(x_1 - x_0)} \right] \tag{3.11}$$

3.3 Water vapour generation

Taking from reference [8] the following:

The weight of evaporate (3.12)

$$W_{Water}^{Evaporate} = W_{Sucrose}^{Base} \left(\frac{1}{C_{Nectar}} - \frac{1}{C_{Honey}} \right) = W_{Sucrose}^{Base}\,\xi \tag{3.12}$$

In terms of the rate of production of honey (3.13)

$$\dot{W}_{Water}^{Evaporate} = C_{Honey}\,\dot{W}_{honey}^{Base}\,\xi \tag{3.13}$$

The weight of nectar metabolised (3.14)

$$\dot{W}_{Nectar}^{Evaporate} = \frac{L_{water}\,\dot{W}_{Sucrose}^{Base}\,\xi}{C_{Nectar}\,L_{Sucrose}\,\Gamma_{Thermal}} = \frac{C_{Honey}\,L_{water}\,\dot{W}_{Honey}^{Base}\,\xi}{C_{Nectar}\,L_{Sucrose}\,\Gamma_{Thermal}} \tag{3.14}$$

The volume of nest nectar consumed for other purposes is derived from the mass of the colony and the metabolic rate (3.15).

$$\dot{W}_{Nectar}^{Nest} = \frac{\dot{L}_{meta} W_{colony}}{L_{Sucrose} C_{Nectar}} \tag{3.15}$$

By substitution of (3.14) and (3.15) into (2.1) gives (3.16).

$$\dot{W}_{Vapour}^{Total} = \alpha C_{Honey} \dot{W}_{honey}^{Base} \xi + \left[\frac{\dot{L}_{meta} W_{colony}}{L_{Sucrose} C_{Nectar}} + \frac{C_{Honey} L_{water} \dot{W}_{Honey}^{Base} \xi}{C_{Nectar} L_{Sucrose} \Gamma_{Thermal}} \right] \left[\beta_0 (1 - C_{Nectar}) + \beta_1 C_{Nectar} r \right] \tag{3.16}$$

Nectar collection and ripening is subject to the break-even constraint for the energy margin *M* for nectar collection from reference [8] which is maximised when the nectar source is close to the nest, hence (3.17)

$$\frac{L_{Sucrose}}{L_{Water}} \geq \frac{\xi}{\Gamma_{Thermal}} \tag{3.17}$$

Using (3.17) the water vapour rate for the value of TEE that breaks even in energy is given below in (3.18).

$$\dot{W}_{Vapour}^{Total} = \alpha C_{Honey} \dot{W}_{honey}^{Base} \xi + \left[\frac{\dot{L}_{meta} W_{colony}}{L_{Sucrose}} + C_{Honey} \dot{W}_{Honey}^{Base} \right] \left[\beta_0 \left(\frac{1}{C_{Nectar}} - 1 \right) + \beta_1 r \right] \tag{3.18}$$

For colony to be successful then the power consumed by background metabolism must be insignificant compared to the rate at which energy is stored by the colony i.e. inequality (3.19)

$$\dot{L}_{meta} W_{colony} \ll C_{Honey} \dot{W}_{Honey}^{Base} L_{Sucrose} \tag{3.19}$$

Then (3.18) becomes (3.20) the maximum possible water production, Similarly at TEE =1 equation (3.21). Both equations are of form (3.22).

$$\dot{W}_{Vapour}^{Total} \approx C_{Honey} \dot{W}_{Honey}^{Base} \left[\alpha \xi + \beta_0 \left(\frac{1}{C_{Nectar}} - 1 \right) + \beta_1 r \right] \tag{3.20}$$

$$\dot{W}_{Vapour}^{Total} \approx C_{Honey} \dot{W}_{Honey}^{Base} \left[\alpha \xi + \frac{L_{Water} \xi}{L_{Sucrose}} \left(\beta_0 \left(\frac{1}{C_{Nectar}} - 1 \right) + \beta_1 r \right) \right] \tag{3.21}$$

$$\dot{W}_{Vapour}^{Total} \approx C_{Honey} \dot{W}_{Honey}^{Base} \left(\alpha \mathrm{A} + \beta_0 \mathrm{B}_0 + \beta_1 \mathrm{B}_1 \right) \tag{3.22}$$

3.4 Water removal capacity

Assuming the condensing region to be of uniform temperature in equilibrium, the gas volume in the cavity as incompressible, and the amount of energy dissipated via the entrance by advection is negligible [8], then latent heat of condensation is dissipated by the nest walls, giving the energy balance shown in equation (3.23).

$$\dot{W}_{Condensate} L_{water} \le \Lambda_{Con}(T_D - T_{Out}) \, where \, \{T_D \ge T_{Out}\} \tag{3.23}$$

The entrance velocity is described as the product of the maximum air velocity and cubic polynomial function with respect to RH at brood temperature 307.7 K. An RH at a known temperature is related to a dew point temperature T expressed as parameter δ_D by a function derived from equations (3.6)(3.7)(3.8) to give (3.24).

$$\chi = e^{[17.2694(\delta_D - \delta_{Brood})]} \tag{3.24}$$

Substituting (3.24) into the polynomial gives (3.25).

$$u_{Ent}(T_D) = u_{Max}\left[a_3 e^{3[17.27(\delta_D - \delta_{Brood})]} + a_2 e^{2[17.27(\delta_D - \delta_{Brood})]} + a_1 e^{[17.27(\delta_D - \delta_{Brood})]} + a_0\right] \tag{3.25}$$

The total water removal capacity equals the sum of advection and condensation hence equation (3.26).

$$\hat{\dot{W}}^{Total}_{Vapour} = \frac{\Lambda_{Con}}{L_{Water}}(T_D - T_{Out}) + \frac{A_{Ent} u_{Ent}(T_D)}{2}(\rho_{Exhaust} - \rho_{Inlet}) \tag{3.26}$$

Using equation (3.2) for the density of a vapour and (3.1) for the vapour pressure at the dew point T_D, gives (3.27)

$$\hat{\dot{W}}^{Total}_{Vapour} = \frac{\Lambda_{Con}}{L_{Water}}(T_{Out} - T_D) + 0.6615 A_{Ent} u_{Ent}(T_D)\left(\frac{e^{[17.27\,\theta_D]}}{T_D} - \frac{e^{[17.27\,\theta_{Out}]}}{T_{Out}}\right) \tag{3.27}$$

Λ_{Con} and u_{Ent} in equation (3.27) are expanded using (3.25),(3.10), (3.11) and (3.3) for the range of man-made hive and the tree nest cases, and then solved for $T_{D.}$ With T_D known, one can determine the brood zone RH using (3.24).

Brood zone air at humidity $\{\chi_i, T_{Brood}\}$ is elevated to desiccating temperature, T_{Honey}, in the nectar/honey zone at the honey activity χ_{Honey} where $\{\chi_i, T_{Brood}\} = \{\chi_{Honey}, T_{Honey}\}$ As shown in equation (3.28), which is derived from equation (3.8).

$$T_{Honey} = \frac{273.16 - 35.86(\gamma_i + \delta_{Brood} - \gamma_{Honey})}{1 - (\gamma_i + \delta_{Brood} - \gamma_{Honey})} \tag{3.28}$$

4 Results

The honey bee fanning information is derived from honey bee colonies in Pretoria South Africa. As a consequence the climatic data used is from that location.

4.1 Water vapour production

The break-even point values of TEE, where maximum water vapour production occurs, vary with nectar concentration as plotted in figure 5 from equation (3.17). This maximum water production was plotted in In figure 3 and 6. using equations (3.27) and (3.23). This is compared as a ratio to the minimum water production (TEE =1.0) as shown in fig 4 using equation (3.16). The minimum water production is also shown in figure 7 Note: α β_0 β_1 are assumed to have a value of 1 in both figs 3 and 4.

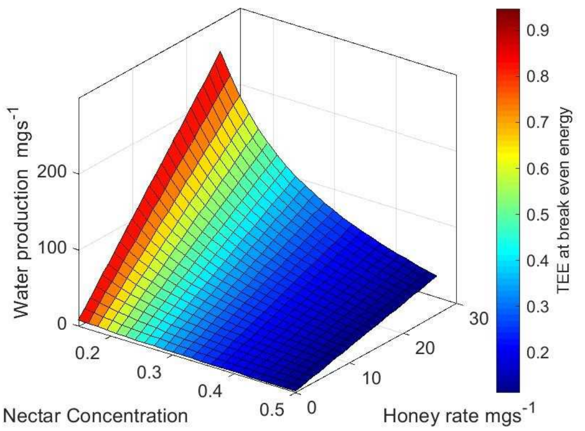

Figure 3: Maximum water product at break-even TEE

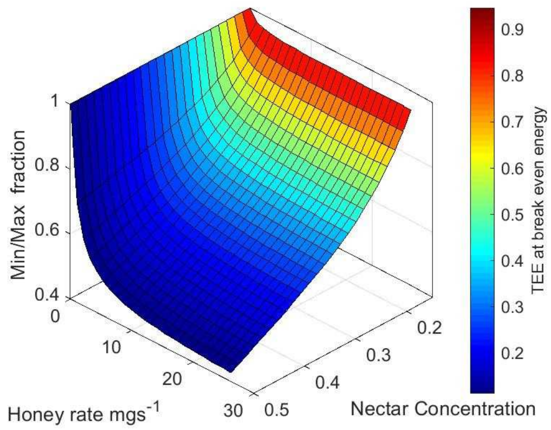

Figure 4: Ratio of minimum to maximum water product (Min: TEE=1, Max: TEE=break-even)

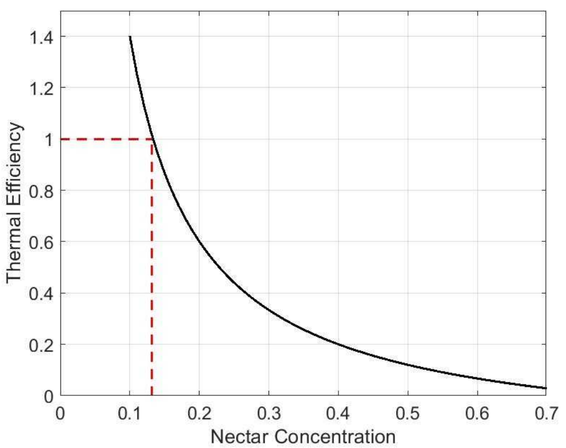

Figure 5: TEE to Nectar concentration at break-even point at zero nest to flower distance

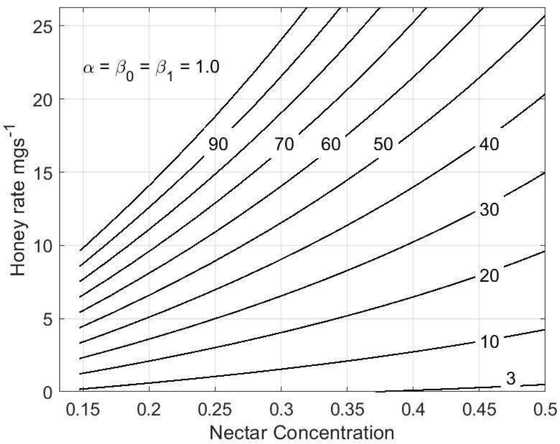

Figure 6: Break-even water production contours mgs^{-1} vs nectar concentration and honey rate

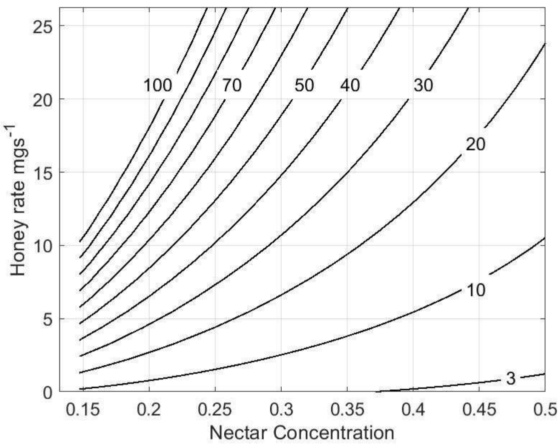

Figure 7: TEE=1 water production contours mgs^{-1} vs nectar concentration and honey rate

Water production is dependant on 3 coefficients α, β0, β1, which are multiplied by the terms A, B_0, and B_1 the relative magnitude of these terms are plotted in: figure 8, for the case of TEE equal to one and fig 9 where TEE is at the break-even value using equations (3.20)(3.22) and (3.21).

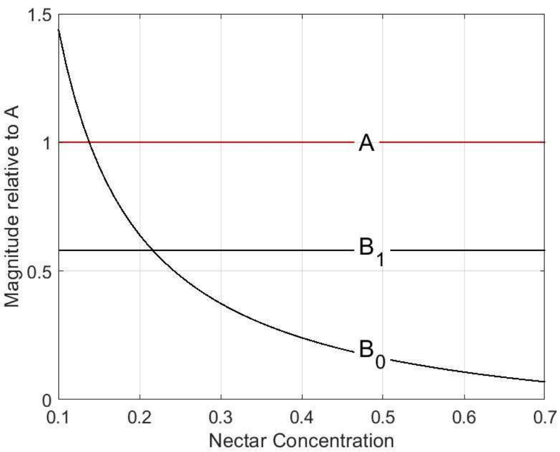

Figure 8: Water Product factors at TEE=1

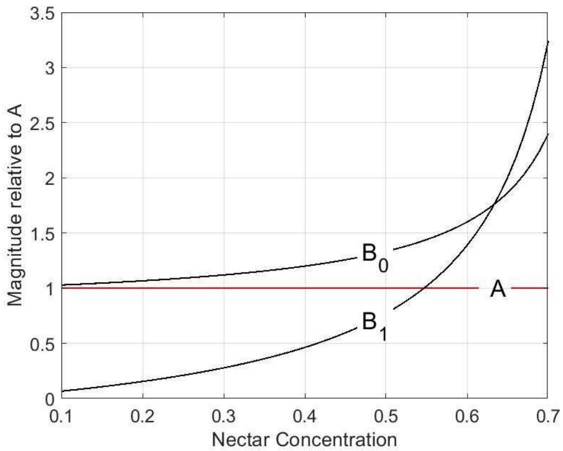

Figure 9: Water Product factors at TEE break-even

4.2 Water vapour removal capacity

The scenarios studied are divided into two nest types; tree with a fixed height cavity and a man-made hive which can have variable height. Each nest type is divided into 4 combinations of high and low lumped thermal conductance, small and large entrances. The entrance and nest dimensions are taken from sources [4,18]. Equations (3.10)(3.11) provide conductances as shown in table 2.

Using equation (3.27), one can then calculate the water vapour that can be removed by various combinations of entrance and condensation as shown in table 2 where A, B, C, & D represent the limits of conductance and entrance area for a tree nest and E, F, G, & H for man-made hives. The water removal capacity is tabulated at two levels of humidity 4.3 kPa and 4.9 kPa. The spread of conductance and entrance area is shown in figure 12 against the contours of water removal at 4.9 kPa. The brood zone humidity versus water removal capacity is plotted in the figures 10 and 11. The humidities of: optimal egg survival; the upper limit of varroa breeding success; Miami USA; summer Pretoria SA and winter Pretoria SA are shown for comparison.

The nectar desiccating temperature of the nectar/honey zone was plotted as contours against in the input RH at brood temperature [14]and the resultant honey water content. This was calculated using equations (3.28) and (1.1), and shown in fig 13. The vertical dashed line indicates a typical long term storage water content of 0.2. The horizontal dashed line indicates 4.3 kPa, the upper limit of varroa breeding success.

4.3 Experimental agreement

The analysis indicates lower water vapour removal capacity in tree nests. Thus one may expect to find higher humidities observed compared to hives when nectar ripening activity is not intense. Unfortunately there are no studies available that give sufficient information to infer the rate of water vapour production, however a ZDUPSA study [33] does conduct a simultaneous measurement of humidity in both trees and man-made hives. It is reasonable to assume similar rates of water vapour production, and thus predict the humidity in one environment given the humidity of the other using the model with median conductances for both nests. The observed humidity in the trees in the study was~3.8 kPa {0.7, 307.7 K} which results from ~7 mgs^{-1} of water production according to the model in figure 11. Then using this water production in a median hive, it is predicted that this would produce ~3.0 kPa as shown in figure 10. This agrees with the ZDUPSA experimental values in the range 3.0 kPa to 3.3 kPa.

Further, the model determines that, if the nectar flow is zero or low and fanning is not taking place, the water vapour removal is primarily by condensation. Then the humidity is constrained by the internal nest surface temperature at saturation from equation (3.23) i.e. dew point. In the high conductance hives this will be within a few degrees of the outside air temperature i.e. { 1.0, ~T_{Out}}. ZDUPSA conducted two humidity studies in winter [31,33] in average ambient temperatures of 288 K. The elevation of inside temperature above ambient for wooden hives in cool winter configuration is around ~5 K [4] and less in warmer ambient temperatures. The model predicts then that the nest humidity will be about {1, 288+5} equal to {1, 293 K} or 2.3 kPa. The average observed humidity in the ZDUPSA experiment was between 1.9 kPa {0.35, 307.7 K} and 2.5 kPa {0.45, 307.7 K}. Another similar, earlier study in the UK [45] showed the internal dew point 7 degrees higher than the external winter ambient temperature, which again concurs with the model.

				Water removal mgs^{-1}	
#	Nest Description	A_{ent} cm^2	Λ_{Con} WK^{-1}	(a)	(b)
A	Tree nest low conductance, small entrance	7.5	0.4	5.6	9.8
B	Tree nest low conductance, large entrance	15	0.4	9.8	17.9
C	Tree nest high conductance, small entrance	7.5	2	10.9	16.4
D	Tree nest high conductance, large entrance	15	2	15.1	24.5
E	Man-made hive, no shallows, small entrance	6.5	2.5	11.9	17.5
F	Man-made hive, no shallows large entrance	83	2.5	55.6	100.2
G	Man-made hive, 4 shallows small entrance	6.5	12	43.4	57.1
H	Man-made hive, 4 shallows large entrance	83	12	86.7	139.8

Table 2: Water removal capacity of Nest limits of conductance and entrance area, at water vapour contents (a) 4.3 kPa and (b) 4.9 kPa.

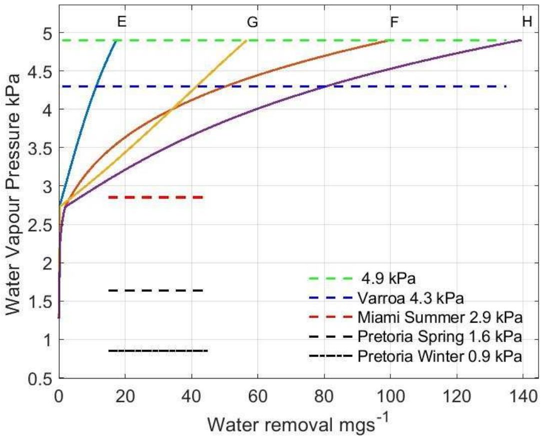

Figure 10: Man-made hive brood zone humidity

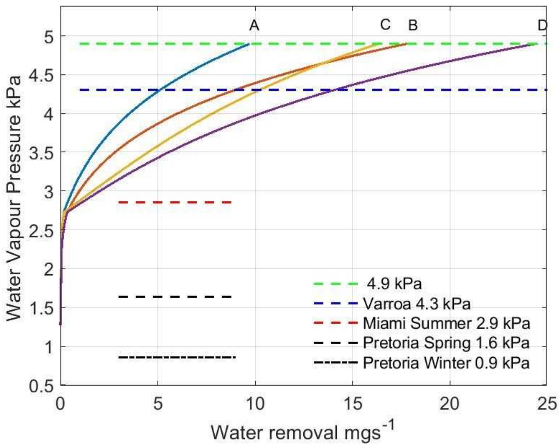

Figure 11: Tree nest brood zone humidity

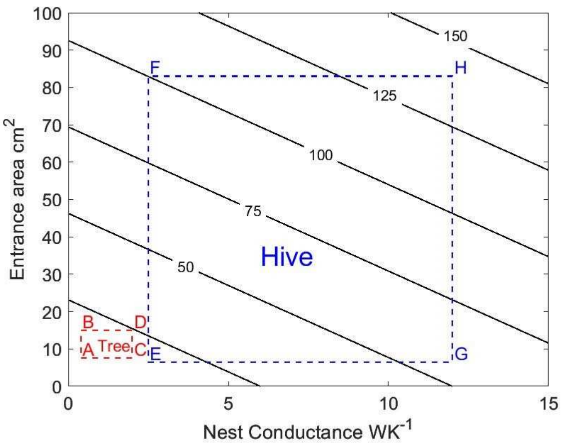

Figure 12: tree and man-made nest limits plotted onto contours of water removal vs nest conductance and entrance area.

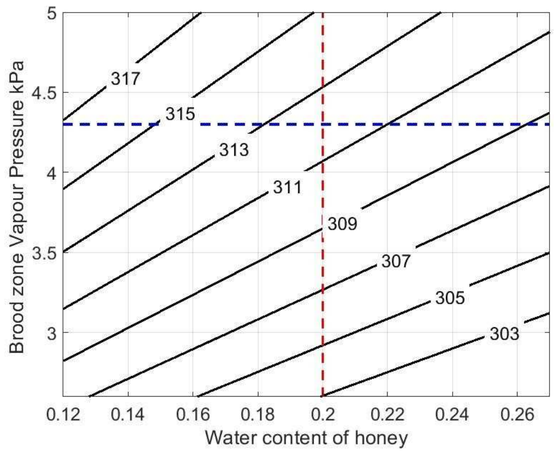

Figure 13: Contours of nectar/honey zone nectar desiccating temperature vs water content, $1-C_{Honey}$ *and brood zone vapour pressure.*

5 Discussion

This is a zoned steady state analysis of the averages of micro climates within the zones, thus extrapolating what occurs during the daily cycle is open to errors owing to thermal diffusivity, commonly known as thermal inertia. Thus internal humidity changes due to condensation will follow, but lag behind and be less severe than predicted from the external daily temperature changes depending on the construction, contents of the nest and amount of insolation. This lag and averaging out will be most pronounced in the high thermal capacity and low conductance of tree nests. Further, water production and removal is not completely synchronous, as average nest humidity increases following foraging activity and then decreases with time as nectar desiccation proceeds, often at night, after the cessation of foraging.

There is considerable further work in finding: data on thermal diffusivity and time-varying nectar gathering and desiccation rates, to populate a more accurate transient based analysis; factors governing microclimates within the zones, to determine their limits. However, this analysis should be sufficient to act as an aid to interpreting the daily rise and fall of hive humidity.

5.1 Factors in Water Production

During nectar desiccation the overwhelming majority of the water vapour in the nest is a direct consequence of the nectar desiccation, the water vapour from the rest of the hives nectar consumption and metabolism becomes an insignificant factor, as can be seen in figures 6 and 7 from the values of contours that cross the zero honey rate-axis.

TEE has a profound effect on water production as can be seen in the degree of variation between maximum and minimum values shown in figure 4, where for typical concentration ranges (0.2 - 0.4) and honey ripening rates 5 mgs^{-1} to 15 mgs^{-1} the minimum to maximum ratio is 0.5 to 0.75. TEE also has a limiting effect on usable nectar concentration. If one looks at figure 5, for the value of TEE equal to 1, the corresponding nectar sugar concentration is 0.132 $KgKg^{-1}$. This value provides an indication of the lowest level of nectar resource that is of long term use to honey bees even in the most favourable conditions.

To understand the importance of the various sources of water within the nest, one needs to compare their relative magnitudes as shown in figures 8 and 9. These show the relative magnitudes of the terms (A, B_0, B_1) that are multiplied by the coefficients (α, β_0, β_1). When TEE is equal to one, see figure 8, it reflects a scenario where the external temperature is close to that inside the nest i.e. tropical. In contrast, figure 6 is a colder climate, high heat loss scenario at the break-even point, where the colony is at its most stressed. In the “tropical” scenario one can see that B_1 and B_0 both remain smaller than A except at very weak concentrations. The “colder” scenario however, has a high relative value for B_0 throughout the concentration range. This indicates the water content of nectar used as fuel to desiccate the honey is a significant contributor of water in the nest. The magnitude of B_0 means the coefficient β_{0c}, the vapour fraction of nectar fuel water content, is an important value for the science related to honey bees in colder climates. Unlike α, β_0 can currently only be inferred and assumed.

5.2 Humid brood zone, dry nectar honey zone

Honey bees appear on first inspection to have conflicting requirements of a high temperature humid brood zone and dry air needed for nectar desiccation. If one looks at figure 13, one can see that if the humid air from the brood zone is heated it can desiccate nectar to low moisture levels. If air containing 4.3 kPa of water is than heated to 312 K then it will desiccate nectar to produce honey with only 20% water. This water content is low enough to prevent microbial growth in the honey and the vapour pressure is high enough to hinder the breeding of varroa. This fulfils both the need to have a long term food supply and to reduce the impact of this parasite.

In this model these zones are separated, however for honey bees this may not be easy to achieve, particularly in low aspect ratio man-made hives, where thermal stratification is not strong and is often disturbed by bee keepers.

5.3 High humidity required, low found in man-made hives

There is a marked contrast in humidity between in-vitro honey bee rearing 4.1 kPa [22] and man-made hives 2.2 kPa to 3.3 kPa [31,45]. In the latter the humidity is measured outside the micro climates in the cells maintained by the nurse honey bees. If *A. mellifera* optimally evolved for tree dwelling then maintaining such difference between the general humidity and the micro climates must therefore represent a stress condition. The difference arises from the condition that unless there is very high water production rates then internal humidity in high conductance, large entrance hives is tied down to $\{1, T_{Out}\}$ (dew point ~ outside temperature) and when large top vent/entrances are added then it is tied to $\{\chi_{Out}, T_{Out}\}$

5.4 Hives good for Varroa, tree nests good for Honey bees

That high humidities particularly in cooler climates require low thermal conductance enclosures has been discussed in relation to varroa in other work [4] and is an accepted thermofluid phenomenon [46]. In addition, the possible impact of top vents or entrances, using recent thermofluid models [47], has also been discussed [48].

The common practice of man-made hives of thin walled wooden construction with many shallows on top is shown in the high conductance scenarios (limits E, F, G, & H) which result in much higher lumped thermal conductances than tree nests (limits A, B, C, & D) of 2.5 to 12 WK^{-1} vs 0.4 to 2.0 WK^{-1}. This and the very much larger entrances used in summer (limits F, H) tie the humidity close to {1, T_{Out}} at low water production rates and increase the water production rate needed to reach 4.3 kPa, by a factor of five as can be seen in figures 10 and 11 (i.e. 50 mgs^{-1} vs 10 mgs^{-1})

Taking nectar concentration of 0.33, typical of oil seed rape, a common European honey producing crop, one can see from figures 6 and 7 that these water production rates imply honey production rates of 12 to 25 mgs^{-1} for a man-made hive and 1 to 3 mgs^{-1} for a tree nest. This means honey bees, in man-made hives, need to forage and desiccate honey at 10 times the rate to obtain the 4.3 kPa humidity sufficient to affect varroa fecundity. The foraging conditions, needed for these honey production rates will occur less frequently than those required by the modest rates needed by tree nests.

Counter-intuitively, a sub tropical climate, such as Florida, is not sufficient. The common practice of using high conductance, top vented hives [49,50], ties internal humidity to the outside, which in a Florida summer averages at 2.8 kPa {0.72, 301 K}[51]. At low water production levels, in this climate and hives, but without top vents, humidity will only accumulate to circa 3.8 kPa, allowing varroa to proliferate.

However, with a sustained average outside temperature of above 303.2 K, e.g. warm dessert areas of southern Algeria, the analysis shows a high conductance hive, without top vents, can accumulate 4.3 kPa. This may account for the reported higher brood infestation in northern compared to southern Algeria [52] where, in the south, for large parts of the year, the average ambient temperature is above 303.2 K [53]; yet in the north, the average summer temperature is 298 K [38] with a corresponding hive humidity of 3.2 kPa.

In addition, better nectar sources and higher external temperatures, factors shown in this analysis to give higher nest humidity, have been positively correlated with reduced varroa infestation in an experimental research of Mediterranean apiaries [54]

Thus changes to bee keeping practice can improve the frequency of varroa disrupting high humidity for man-made hives: improved foraging, avoiding top vents, constructing hives from lower thermal conductivity materials, having fewer shallows on the hive by more frequent harvesting and matching entrance size to water removal demand by changing the entrance size in response to changing internal humidity or ripening activity.

6 Conclusion

The thermofluid physics in the production and removal of water vapour bound the behaviours of the honey bee colony. Within the constraints of its steady state, averaging approach and assumptions, this theoretical analysis explores those boundaries and has found:

- Honey bees must produce and dispose of considerable quantities of water vapour in order to convert nectar into honey. Typically 4 to 7 times the weight of honey.
- Climate is a major factor especially when cooler climates are combined with high conductance hives. The fuel used in nectar desiccation then becomes the dominant source of water vapour in the nest.

- The thermal conductance of the nest and the dimensions of the entrance have a major impact on nest humidity. This makes high humidity a much more likely and frequent occurrence in tree nests and the low humidity found in man-made nests a likely stressor.
- Low humidities observed in some hives may be a direct result of their construction and thermal conductance.
- Hive thermal conductance and entrance size can potentially change the impact of varroa on honey bee colonies.
- Top vents can tie inside to outside humidity, which even in subtropical climates is substantially below the ideal for larval growth and the reduction of varroa fecundity. Therefore, they may increase the levels of honey bee stress and the likelihood of varroa infestation.

Finally, this study shows, through changing hive design and bee keeping practices, how to achieve the absolute humidity level of 4.3 kPa (~30 gm^{-3}), that makes varroa fecundity fall.

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8 Competing interests

The author has no competing interests.

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