Thermal efficiency extends distance and variety for honey bee foragers: Analysis of the energetics of nectar collection and desiccation by Apis mellifera

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Abstract

The desiccation of nectar to produce honey by honey bees (*Apis mellifera* L.) is an energy intensive process, as it involves a quasi-isothermal change in the concentration of sugars from typically 20% to 80% by vaporisation (honey ripening). This analysis creates mathematical models for: the collected nectar to honey ratio; energy recovery ratio; honey energy margin; and the break-even distance, which includes the factors of nectar concentration and the distance to the nectar from the nest; energetics of desiccation; and a new factor, thermal energy efficiency of nectar desiccation (TEE). These models show a significant proportion of delivered energy in the nectar must be used in desiccation and that there is a strong connection between TEE and nest lumped thermal conductance with colony behaviour. They show the connection between TEE and honey bee colony success, or failure, in the rate of return, in terms of distance or quality of foraging. Consequently TEE is a key parameter in honey bee population and foraging modelling. For bee-keeping it quantifies the summer benefits of a key hive design parameter, hive thermal conductance and gives a sound theoretical basis for improving honey yields, as seen in expanded polystyrene hives.

1 Introduction

Honey, a high sugar concentration (>80%) fluid, is desiccated by honey bees from flower nectar, a lower sugar concentration liquid (10% - 50%) and modified by the secretion of enzymes. After collection from numerous flowers, sometimes at the considerable distance of 1 to 9 Km. This nectar is passed by the forager honey bee to another honey bee, an unloader /storer, which 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, while the hive population engages in vigorous forced air movement within the nest by fanning their wings [1–3].☐ The first part of the process, lasting a few minutes, the second part, a few hours up to a few days. This activity takes place with considerable intensity during summer evenings, it is clearly audible (i.e. greater than 30 dB) from a distance of several metres, and can last into the small hours of the following morning. The efficiency of this process is vital for the honey bee colony to survive periods when no nectar is available, especially during winter. *A. mellifera* does not hibernate in winter, but uses the stored energy in the honey's sugars to maintain temperatures above 18C for some of the colony, and above 10C for the remainder, when temperatures outside the nest enclosure can be as low as -40 C [4–6].

The amount of water evaporated can be more than 400 kg per year. Considerable amounts of energy of the order of 1GJ are required to achieve this, given the very high latent heat of evaporation of water of 2.426MJkg^{-1} at 305K [7,8].

This is a normal, routine operation in the nest and hence a factor in the thermoregulation of the colony. In the numerous discussions on how water is collected and used for thermoregulation [9–14]□ , the only parallels drawn between water and nectar are in the use of the proboscis. The water content of the nectar is referenced as a resource of water for brood [13]□.

Studies of honey bees under heat stress (simulated heat waves)[14] have noted honey bee nectar collection behaviour changes to collect more dilute nectar. The authors attributed this as a means of providing more resources for collection of water for thermoregulation.

Thermoregulatory temperature transitions after feeding with nectar would be expected as desiccation proceeds i.e. temperature increases to reduce relative humidity (RH) followed by rapid decreases towards the end of the evaporation phase. These have been observed [15]□ but, to date, not attributed to nectar desiccation.

The literature on honey bee population, thermoregulation and foraging e.g. [15,16,25–34,17,35–44,18–24]□ say nothing about the thermal efficiency or detail about the energy of nectar desiccation, theoretical or experimental. An older source on honey ripening [45] gives the weight of nectar required to ripen a pound of honey at 40% nectar concentration and opines that this energy is largely sourced from insolation and the ambient air. This is the only article found by the author that considers the magnitude of the energy requirement of desiccation.

The literature includes works on:

- Energy efficiency of honey production [20]□
- Predicting honey yields from nectar sources [21–23,38]□.
- Models of honey bee population [24–31,39]□□□□
- Honeybee foraging strategies and costs [16,33,44,34–37,40–43]□□□□□

Their assumptions, not always explicit, include:

1. *Population overhead* – The energy cost is dependant only on the number of insects assigned to the processing or the hive population in general [25,27,35]□.

2. *Direct energy equivalence* **–** The value of the energy in the nectar is identical to that stored in the honey [26,30,33,39]□, or that conversion cost is not significant [16,34]□.

3. *Nectar not honey as stored energy* – “Stored nectar” rather than honey as the stored energy medium [40]□.

For Northern European honey bees (e.g. *A.m.mellifera, A.m. Iberiensis, A.m.ligustica*) in a temperate climate, nectar concentration during flight does not occur [1]□. This contrasts with *A.m.scutellata* in hot arid climates [46]□, where energy is gained in flight from the air and insolation.

While insolation may input energy in high thermal conductance (2.6 WK^{-1}) man-made hives in full sun, *A.mellifera*, in nature, resides in shaded, very low thermal conductance nests (0.4 WK^{-1}) [47] [48]□. In both types of nest, in temperate climates, vigorous nectar evaporation takes place at night. Thus we may rule out insolation as a necessity for desiccation. Thus for honey bee metabolic heat, conduction and advection are on the right hand side of the heat balance equation below (equations (22) and (3)), and the energy required to desiccate the nectar on the left.

$$\dot{E}_{Evaporate} = \dot{q}_{bee} + \left(\Lambda_{Nest} + \frac{1}{2}A_{Entrance}\kappa_{Air}\rho_{Air}u_{Entrance}\right)(T_{Outside} - T_{Inside}) \quad (1)$$

Typical values for the lumped conductance range from 0.4 WK^{-1} for tree nests, and 2.5 WK^{-1} for man made nests. Typical values for entrance size and fanned air velocity are 25 cm^3 [4]) and 1 ms^{-1} [49] . These give an advection term of around 1mWK^{-1}, thus we can ignore the energy in the advection caused by honey bees fanning at the entrance.

In temperate climates, the nest temperatures are usually significantly higher than ambient [4]. Given the above analysis and observations, one may discount the outside environment as being a major contributor of energy to desiccation, and is instead more likely to be a potential loss . This scenario forms the focus in this analysis.

The energy released by the honey bees converting disaccharide sugars to monosaccharides has been postulated as a source of energy, but this is insignificant compared to the energy required in the evaporation process amounting to only ~15 $kJmol^{-1}$, or ~43 $kJkg^{-1}$ [50].

The metric in the literature [39,52,53] for assessing the continuing survival of a honey bee colony is the margin of return on the energy spent by the honey bees foraging. It was defined as the energy recovered minus the total energy expended divided by the energy expended. Long term survival is considered only to be likely when this metric is greater than zero. This was concerned with how much of the energy available, in all of the reachable or visited flowers, is delivered to the hive entrance. It did not account for how energy is made available for consumption as honey, considering that nectar starts to become honey within minutes after the forager arrives back at the nest [45].

This analysis provides the physics that constrains the biological behaviours of the honey bees providing the basis for new hypotheses, insights and understanding for those behaviours. The magnitude of the energy involved in the desiccation process, and how the losses and efficiency impact the honeybee colony are the focus of this study.

2 Approach

2.1 System Boundary

A system boundary defines the scope of an energy transfer analysis. For example previous studies have taken this boundary as:

- Only the colony of honey bees [5]
- The Individual honey bees, from the hive entrance to all of the individual flowers and back again [51]

Analysis considers the energy inputs and outputs of the system across the boundary as well as any change of state of the system e.g. from a liquid to a vapour.

This analysis will consider the system to be bounded by the nest enclosure, which loses heat, determined by the lumped conductance of the nest, and the outside temperature and the journey to and from the flower patch from the nest in the absence of wind. This approach has been chosen to focus on the colony and nest impacts rather than impacts and dependencies of the flowers. This focus involves factors of nectar desiccation and distance flown to forage areas as opposed to flower patch depletion or honeybee time spent. As a consequence it excludes the flower to flower transport energy which is assumed to be replaced at the flower patch.

The nest consumption of honey e.g. the up keep of the nest, brood etc. are considered as an energy drain after the desiccation process and therefore fall outside of the analysis.

Water and pollen collection are significant activities for the honey bees involving expenditure outlay and return, however for this analysis, we assume that the nectar collection is the dominant energy input process which is borne out by the relative quantities and calorific gains [4].

2.2 Thermal energy efficiency of nectar desiccation

Losses from a system and the useful work done are usually treated as an efficiency coefficient. Defined as the ratio of energy or work, that is useful to the goal, divided by the total energy input in trying to achieve that goal. In this application this quantity, $\Gamma_{thermal}$, is shown in equation (2).

$$\Gamma_{thermal} = \frac{E_{Evaporate}}{\left(E_{Evaporate} + E_{Losses}\right)} = \frac{E_{Evaporate}}{E_{Evaporate}} \qquad (2)$$

The losses in equation (2) are dominated by the lumped nest conductance. The thermal efficiency of nectar desiccation is dependent on the lumped conductance of the nest, the averaged temperature difference between the inside and outside of the nest, and the rate of water being evaporated as shown in equation (3).

$$\Gamma_{Thermal} \approx \frac{1}{\left(1 + \frac{\Lambda_{Nest}\left(T_{Inside} - T_{Outside}\right)}{\dot{E}_{Evaporate}}\right)} \qquad (3)$$

Important:

- The lumped thermal conductance includes the internal and external convective heat transfers, as well as the conduction through the nest envelope. The first and second are dependent on flow velocity and local geometry (equation (22)).
- If the outside temperature is above the internal temperature, then the thermal efficiency will be greater than 1, because there is heat gain rather than loss.

2.3 Metrics

In the current analysis, the honey energy margin (HEM) is the sum of the energy costs the honey bees cannot immediately replace in the field $\sum E_{costs}$, subtracted from energy of the honey ripened E_{Honey}, divided by the sum of the energy costs as shown as M in equation (4).

$$M = \frac{E_{Honey} - \sum E_{costs}}{\sum E_{costs}} \qquad (4)$$

Break even distance occurs when the expenditure on transport and desiccation consumes all of the energy collected by the honey bees i.e. when HEM is zero in equation (5), then honey bees cannot accumulate the stores needed for times of dearth e.g. droughts, poor weather and winter.

$$\exists d where M\left(d, \Gamma_{Thermal}, C_{Nectar}, C_{Honey\dots}\right) = 0 \tag{5}$$

The transported energy ratio$\Gamma_{transport}$, is the energy delivered to the entrance divided by the sum of the energy delivered $E_{Delivered}$, and the energy consumed in travelling to and from he flower patch$E_{Transport}$. This metric determines the impact of fetching the nectar from a distance. Similarly to HEM, we will exclude the flower to flower flight costs. However, some of the more complex models, as related in the literature, can be included as part of further study by using a modified transport efficiency ratio that takes those factors into account.

$$\Gamma_{transport} = \frac{E_{Delivered}}{E_{Delivered} + E_{Transport}} \tag{6}$$

Energy consumption on the flight to the flower patch and back depends on numerous factors such as: distance, take-off weight [52]☐, crop content temperature [53]☐, ambient wind speed [54]☐, ambient temperature [55,56]☐. To cater for this complexity, the formulae in the analysis use a single parameter φ with dimensions of $Wkg^{-1}m^{-1}$. However, the results below, following other researchers [34] , use a simplified form. This is derived from the averaged flight metabolic rate and averaged flight speed.

Energy recovery ratio$\Gamma_{Recovery}$, is the energy in the honey accumulatedE_{Base}, divided by the energy in the nectar collected from the flowers$E_{Collected}$, in equation (7). This gives the proportion of useable energy compared to the losses from desiccation and transport. In prior studies this is effectively assumed to be a fixed value of 1.0 at zero nest to nectar distance.

$$\Gamma_{Recovery} = \frac{E_{Base}}{E_{Collected}} \tag{7}$$

Desiccation energy fraction is the fraction of the energy delivered to the nest that is used in the desiccation process. This can be derived from the energy recovery ratio evaluated for zero distance. Hence equation (8)

$$\Gamma_{Dessicate} = \frac{E_{Deivered} + E_{Base}}{E_{Delivered}} = 1 - \Gamma_{Recovery}(d = 0) \tag{8}$$

The Collected nectar to honey ratio$\Pi_{Base,Honey}^{Collected,Nectar}$, is the weight of nectar collected$W_{Nectar}^{Collected}$, divided by the weight of honey after desiccation W_{Honey}^{Base}, shown in equation (9). This enumerates the increase in honey bee trips needed to allow for desiccation and transport losses.

$$\Pi_{Base,Honey}^{Collected,Nectar} = \frac{W_{Nectar}^{Collected}}{W_{Honey}^{Base}} \tag{9}$$

3

4 Nomenclature

Term	Description	Units
$A_{Entrance}$	Cross sectional area of entrance	m^2
C_{Nectar}	Concentration of nectar	$kgkg^{-1}$
C_{Honey}	Concentration of honey	$kgkg^{-1}$
d	Distance from the nest to the flower patch	m
$d_{BreakEven}$	Distance from the nest to the flower patch the result in zero energy gain in honey stored	m
E_{Base}	Energy in resultant honey	J
$E_{Collected}$	Energy in the collected nectar	J
$E_{Evaporate}$	Energy required for evaporation excluding losses	J
$\dot{E}_{Evaporate}$	Rate of energy (power) required for evaporation excluding losses	W
$\bar{E}_{Evaporate}$	Energy required for evaporation including losses	J
E_{Flight}	Energy required for transport	J
E_{Losses}	Energy lost from desiccation process	J
$E_{Sucrose}$	Metabolic energy of sucrose	J
F_x	Dimension set of an air flow x	-
HEM	Honey energy margin	-
L_{Flight}	The energy per kilogram of nectar delivered required for flight from the nest to the nectar flower patch and back	Jkg^{-1}
L_{Honey}	Metabolic value of honey per unit weight	Jkg^{-1}
L_{Honey}^{Nectar}	Latent heat of vaporisation of nectar to honey	Jkg^{-1}
$L_{Sucrose}$	Metabolic energy of sucrose per unit weight	Jkg^{-1}
L_{Water}	Latent heat of vaporisation per unit weight of water	Jkg^{-1}
M	Honey energy margin from collection to honey	-
P_x	Property set of an air flow x	
$\dot{q}_{Advection}$	Rate of nest heat loss by conduction	W
$\dot{q}_{Bee}$	Rate of metabolic heat input by the honey bees	W
$\dot{q}_{Conduction}$	Rate of nest heat loss by advection though the entrance	W
T_{Inside}	Temperature of air inside nest	K
$T_{Outside}$	Temperature of air outside nest	K
TEE	Thermal energy efficiency of nectar desiccation	-

Term	Description	Units
$\overrightarrow{u_x}$	Air velocity of flow x	ms^{-1}
$u_{Entrance}$	Air velocity through entrance	ms^{-1}
W_{Honey}^{Base}	Weight of the resultant honey	kg
W_{Nectar}^{Base}	Weight of resultant base honey in the form of nectar before desiccation	kg
$W_{Sucrose}^{Base}$	Weight of the sucrose within the resultant honey	kg
$W_{Nectar}^{Collected}$	The weight of delivered nectar plus net nectar used in transport	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
$W_{Sucrose}^{Evaporate}$	Weight of sucrose required to evaporate water content of nectar	kg
$W_{Water}^{Evaporate}$	Weight of water to be evaporated	kg
W_{Nectar}^{Flight}	The weight of nectar required as fuel for flight	kg
$\dot{W}_{Water}^{Evaporate}$	Rate of water evaporated in honey ripening	kgs^{-1}
$\dot{W}_{Honey}^{Base}$	Rate of honey ripening in terms of resultant honey	kgs^{-1}
$\Pi_{Base,Honey}^{Collected,Nectar}$	Ratio of the weights of nectar collected to the resulting honey	-
$\Gamma_{Recovery} \equiv \Gamma_{Collected}^{Base}$	Energy recovery ratio: energy in honey divided by energy in collected nectar	-
$\Gamma_{Transport} \equiv \Gamma_{Collected}^{Delivered}$	Transported energy ratio: energies of nectar delivered divided by nectar collected	-
$\Gamma_{Thermal} \equiv \Gamma_{\langle Evaporate \rangle}^{Evaporate}$	Thermal efficiency of desiccation : ratio of $E_{Evaporate}$ divided by $E_{\langle evaporate \rangle}$	-
$\Gamma_{Dessicate}$	Desiccate energy fraction, the proportion of energy delivered used in nectar evaporation	-
$\xi = \Pi_{Base,Sucrose}^{Evaporate,Water}$	Reciprocal concentration of honey subtract from reciprocal concentration of nectar	-
$\zeta = \Pi_{Base,Sucrose}^{Delivered,Nectar}$	Ratio of weights of delivered nectar to base sucrose	-
φ	Energy for flight per unit weight and distance	$Jkg^{-1}m^{-1}$
κ_{Air}	Heat capacity of air	$JK^{-1}kg^{-1}$
ρ_{Air}	Density of Air	kgm^{-3}
Λ_{nest}	Lumped thermal conductance of the nest enclosure e.g. hive, tree etc	WK^{-1}
$\Lambda_{Advection}^{x}$	Convection conductance for flow x	WK^{-1}
$\Lambda_{Advection}^{External}$	External convection conductance	WK^{-1}
$\Lambda_{Advection}^{Internal}$	Internal convection conductance	WK^{-1}

Table 1: Nomenclature

5 Analysis

5.1 Assumptions

The assumptions in this analysis are:

1. The product of a TEE factor and energy required to be generated by the honey bees for evaporating the water from the nectar, including losses, equals the product of the latent heat of vaporisation and the mass of water vaporised.

2. The system boundary is as defined in section 3.

3. The system is in equilibrium i.e. steady state.

4. The honey bee can refuel at the nectar source and that the nectar concentration the honey bee uses as fuel is the same as the nectar source.

5. Nectar concentration does not change in flight i.e. temperate climate [1,46]

6. No variation in energy consumed due to in flight changes in insect weight or wind speed.

7. Enthalpy of evaporating water from nectar to honey is assumed to be constant for all of the starting nectar concentrations over the range 10% to 50% with a finishing honey concentration of 80% and to be approximately that of water [8].

8. Calorific value of the sugars in the honey and nectar are taken to be that of sucrose [50].

9. The enthalpy of inverting sucrose to fructose and glucose and its use of water are negligible, compared to the volume of evaporated water and the energy needed to vaporise it [50].

10. Radiation or changes in external RH are not taken into account.

11. All advection and conduction heat losses are attributed to nectar desiccation for the purposes of thermal efficiency estimation.

12. Dominant process of energy collection is that of nectar. Water and pollen collection are therefore not considered.

13. Nectar sources are considered to be effectively at a single distance and concentration and do not deplete.☐

5.2 Basics

Basic relations and notations are shown below

1. Notation

G_B^A attribute G of quantity A of substance B. e.g $W_{Nectar}^{Collected}$ is weight of collected nectar (10)

2. Ratio of weights notation

$$\Pi_{X,Y}^{A,B} = \frac{W_B^A}{W_Y^X}, \forall X \forall Y \forall A \forall B \text{ where names A and X are quantities, B and Y substances} \quad (11)$$

3. Ratio of energies notation

$$\Gamma_X^A = \frac{E_A}{E_X}, \forall A \forall X \text{ where names A and X are quantities} \quad (12)$$

4. Concentration of substances referenced to sucrose

$$W_Y^X = \frac{W_{Sucrose}^X}{C_Y}, \forall X \forall Y \text{ i.e. for all quantities X, substances Y} \quad (13)$$

5. Mass, energy and latent heats of flight, vaporisation and metabolism

$$W_Y^X = \frac{E_X}{L_Y}, \forall X \forall Y \text{ e.g. Mass quantity X of substance Y with Latent Heat } L_Y \quad (14)$$

6. Sum of evaporation energy and losses

$$\not{E}_{Evaporate} = E_{Evaporate} + E_{Losses} \quad (15)$$

7. Thermal efficiency definition

$$\Gamma_{Thermal} \not{E}_{evaporate} = L_{water} W_{Water}^{Evaporate} \quad (16)$$

5.3 Thermal energy efficiency of nectar desiccation

Energy that can be released from the sucrose is given in equation (14). The water needed to be evaporated is the difference in mass between the honey and the nectar (17).

$$W_{Water}^{Evaporate} = W_{Nectar}^{Base} - W_{Honey}^{Base} \quad (17)$$

Equations (13) and (17) which rearranged give equation (18), the mass of evaporated water.

$$W_{Water}^{Evaporate} = W_{Sucrose}^{Base}\left(\frac{1}{C_{Nectar}} - \frac{1}{C_{Honey}}\right) = W_{Sucrose}\Pi_{Base,Sucrose}^{Evaporate,Water} = W_{Sucrose}^{Base}\xi \quad (18)$$

Equations (14) and (18) give the energy for evaporation.

$$E_{Evaporate} = L_{Water} W_{Sucrose}^{Base}\xi \quad (19)$$

Equation (19) expressed as a rate and using (13) gives equation (20).

$$\dot{E}_{Evaporate} = \dot{W}_{honey}^{Base} L_{Water} C_{Honey} \xi \tag{20}$$

Equation (19) substituted in to equation (2) gives equation (21).

$$\Gamma_{Thermal} = \frac{1}{\left(1 + \frac{\Lambda_{nest}(T_{Inside} - T_{Outside})}{\dot{W}_{Honey}^{Base} L_{Water} C_{Honey} \xi}\right)} \tag{21}$$

Important: Λ_{Nest} is an aggregation of a series network, comprising the enclosure and air to enclosure heat transfers as defined in equation (22). From reference [57], these heat transfers are functions of the property set of the air being moved, the air velocity vectors and the dimension set of the formation of the air flow (23). In this case the internal air flow is the result of honey bee behaviour and natural convection.

$$\frac{1}{\Lambda_{Nest}} = \frac{1}{\Lambda_{Enclosure}} + \frac{1}{\Lambda_{advect}^{External}} + \frac{1}{\Lambda_{advect}^{Internal}} \tag{22}$$

$$\overrightarrow{u_x}, F_x, P_x| \rightarrow \Lambda_{advect}^{x}(\overrightarrow{u_x}, F_x, P_x) \tag{23}$$

5.4 Metrics

The total nectar required is nectar to be made in to honey (base amount) plus the nectar used as fuel for the evaporation (24).

$$W_{Nectar}^{Delivered} = W_{Nectar}^{Base} + W_{Nectar}^{Evaporate} \tag{24}$$

Combining equation (19) and (16), then energy required for evaporation is shown in equation (25).

$$\dot{E}_{evaporate} = \frac{L_{Water} W_{Sucrose}^{Base} \xi}{\Gamma_{Thermal}} \tag{25}$$

The sucrose required as fuel can be determined, (26), then expressed as a nectar mass (27).

$$W_{Sucrose}^{Evaporate} = \frac{L_{water} W_{Sucrose}^{Base} \xi}{L_{Sucrose} \Gamma_{Thermal}} \tag{26}$$

$$W_{Sucrose}^{Evaporate} = \frac{L_{water} W_{Sucrose}^{Base} \xi}{L_{Sucrose} \Gamma_{Thermal}} \tag{26}$$

$$W_{Nectar}^{Evaporate} = \frac{L_{water} W_{Sucrose}^{Base} \xi}{C_{Nectar} L_{Sucrose} \Gamma_{Thermal}} \tag{27}$$

This (27) is then added to the base nectar amount, (24), to give a total mass of nectar that needs to be delivered to the hive, and then rearranged as (28).

$$W_{Nectar}^{Delivered} = W_{Sucrose}^{Base} \frac{1}{C_{Nectar}} \left(1 + \frac{L_{Water} \xi}{L_{Sucrose} \Gamma_{Thermal}} \right) = W_{Sucrose}^{Base} \Pi_{Base,Sucrose}^{Delivered,Nectar} = W_{Sucrose}^{Base} \zeta \tag{28}$$

If we take into account the efficiency of nectar collection i.e. allow for the nectar consumed in transportation (a function of distance of nest from nectar source) using the transported energy ratio then we can create an expression for the nectar collection to honey factor, equation (29), using (28).

$$W_{Nectar}^{Collected} = \frac{W_{Nectar}^{Delivered}}{\Gamma_{Transport}} = \frac{W_{Sucrose}^{Base} \zeta}{\Gamma_{Transport}} \tag{29}$$

L_{Flight} is defined as the energy required to deliver payload per unit weight over *d*, the distance to the flower patch from the nest, and back again as defined in equation (30).

$$L_{Flight} = 2\varphi d \tag{30}$$

Using equation (13) the flight energy is in equation (31).

$$E_{Flight} = L_{Flight} W_{nectar}^{Delivered} \tag{31}$$

Then re-expressed as nectar in equation (32) using (13) and (14).

$$W_{Nectar}^{Flight} = \frac{L_{Flight} W_{nectar}^{Delivered}}{C_{Nectar} L_{Sucrose}} \tag{32}$$

Total nectar needed is the sum of delivered and flight fuel in equation (33).

$$W_{Nectar}^{Collected} = W_{Nectar}^{Flight} + W_{Nectar}^{Delivered} \tag{33}$$

By combining equations (33) and (32) gives (34).

$$W_{Nectar}^{Collected} = W_{Nectar}^{Delivered}\left(1 + \frac{L_{Flight}}{(C_{Nectar}L_{Sucrose})}\right) \tag{34}$$

The ratios of the energies and the weights of quantities of the same substance are equal therefore from (34).

$$\Gamma_{Transport} = \Gamma_{Collected}^{Delivered} = \Pi_{Collected,Nectar}^{Delivered,Nectar} = \frac{1}{\left(1 + \frac{L_{Flight}}{(C_{Nectar}L_{Sucrose})}\right)} \tag{35}$$

From equations (35) (28) and (13) we derive the nectar to honey ratio, the multiplying factor for collected nectar versus base honey weight (36).

$$\Pi_{Base,Honey}^{Collected,Nectar} = \frac{C_{Honey}\zeta}{\Gamma_{Transport}} \tag{36}$$

From equations (13) (14), we derive (37)

$$E_{Base} = W_{Sucrose}^{Base}L_{Sucrose} \tag{37}$$

Combining equations (14) and (29), we derive (38).

$$E_{Collected} = \frac{C_{nectar}L_{Sucrose}W_{Sucrose}^{Base}\zeta}{\Gamma_{Transport}} \tag{38}$$

Thus from equations (7), (37) and (38) energy recovery ratio is found in (39).

$$\Gamma_{Recovery} = \Gamma_{Collected}^{Base} = \frac{\Gamma_{Transport}}{C_{Nectar}\zeta} \tag{39}$$

Similarly desiccation energy fraction (40).

$$\Gamma_{Dessicate} = 1 - \Gamma_{Delivered}^{Base} = \frac{1}{C_{Nectar}\zeta} \tag{40}$$

From the definition of HEM in equation (4) derive equation (41).

$$M = \frac{E_{Base} - \left(E_{evaporate} + E_{Flight}\right)}{\left(E_{evaporate} + E_{Flight}\right)} \qquad (41)$$

Equation (41) is expanded from equations (30), (31), (25), (37) to give (42).

$$M = \frac{L_{Sucrose}}{\frac{L_{Water}\xi}{\Gamma_{Thermal}} + 2\varphi d\zeta} - 1 \qquad (42)$$

Rearranging equation (42), one obtains the distance at which $M = 0$, i.e. the break even distance.

$$d_{BreakEven} = \frac{1}{2\varphi\zeta}\left(L_{Sucrose} - \frac{L_{Water}\xi}{\Gamma_{Thermal}}\right) \qquad (43)$$

6 Results

The general parameters in calculating the results can be found in table 2

Item	Value	Source	Item	Value	Source	Item	Value	Source
κ_{Air}	1.2 $JK^{-1}kg^{-1}$	[58]	ρ_{Air}	1 kgm^{-3}	[58]	$A_{Entrance}$	25x 10^{-4} m^2	[60]
$L_{Sucrose}$	16.2 $MJkg^{-1}$	[59]	$u_{Entrance}$	0.94 ms^{-1}	[49]	C_{Honey}	0.8	[4,45]
φ	162.5 $Jkg^{-1}m^{-1}$	[4]	L_{Water}	2.426 $MJkg^{-1}$ @305K	[7]			

Table 2: General parameters

6.1 Thermal energy efficiency of nectar desiccation

Using a rate of honey ripening $\dot{W}_{Honey}^{Base}$ of 5.3 mgs^{-1} [45] from equation (3), one can plot TEE contours versus nest conductance, temperature difference and nectar concentrations (Fig 1). Note that negative temperature differences (ambient > nest) generate TEE greater than 1.

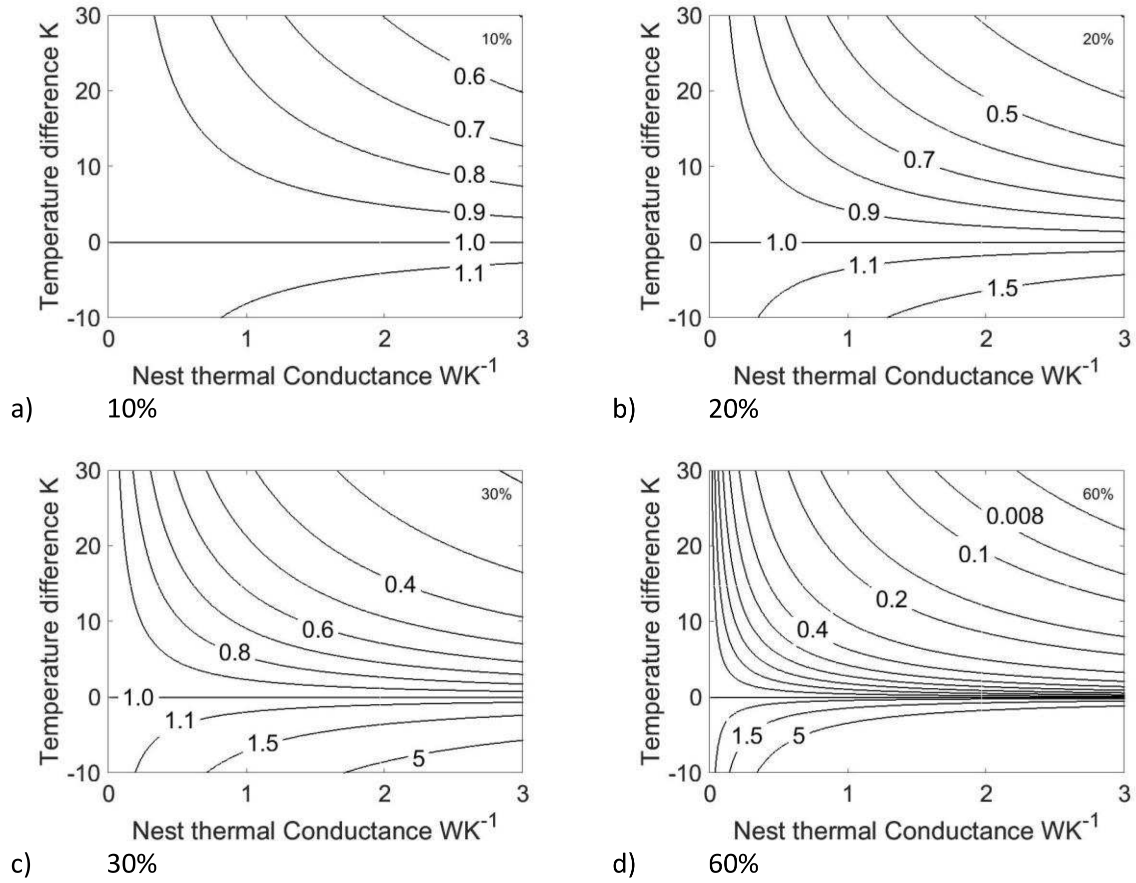


Fig 1: Thermal efficiency (TEE) contours versus nest conductance and internal to external temperature difference for various nectar concentrations (a-d)

6.2 Metrics

From equation (36), one can produce a table of contour graphs at selected distances to the nectar source to produce contours of the factor versus thermal efficiency and nectar concentration in Fig 2 Note: Thermal efficiencies above 1 are included to allow for when temperatures outside greater than inside.

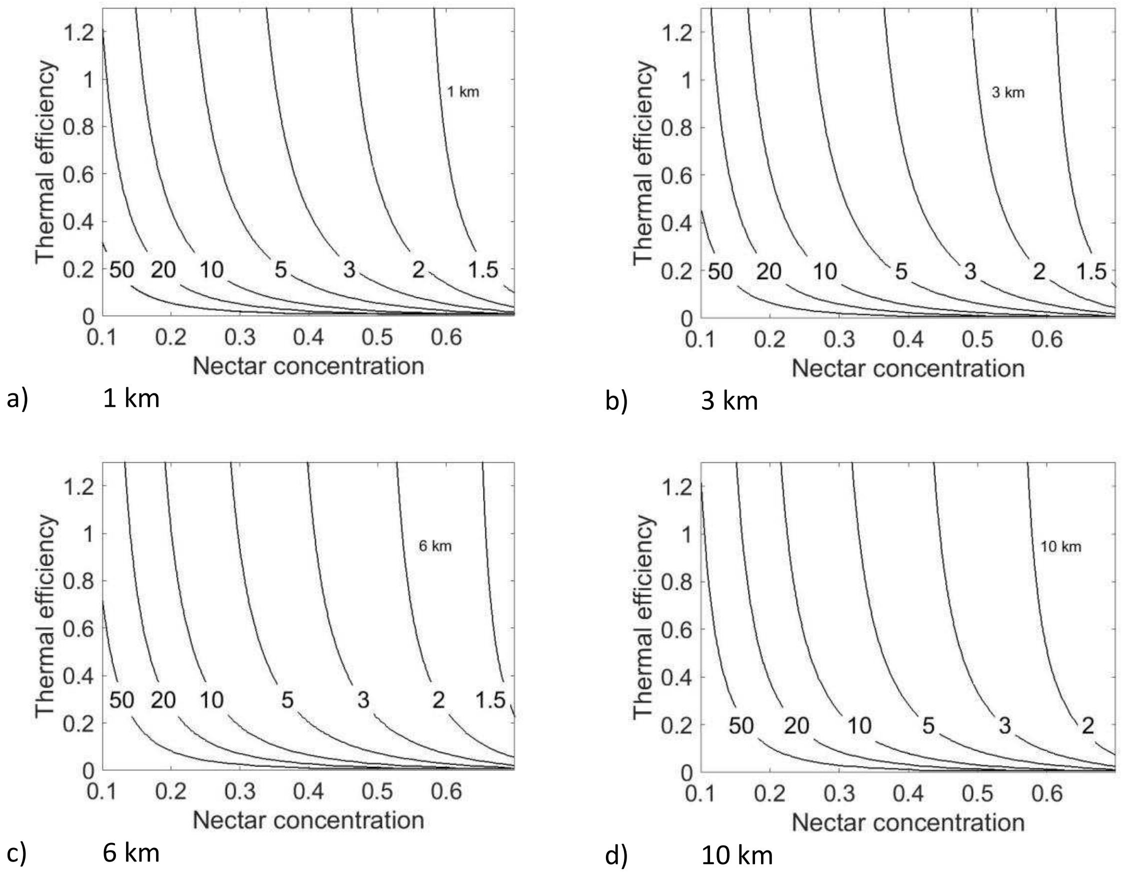
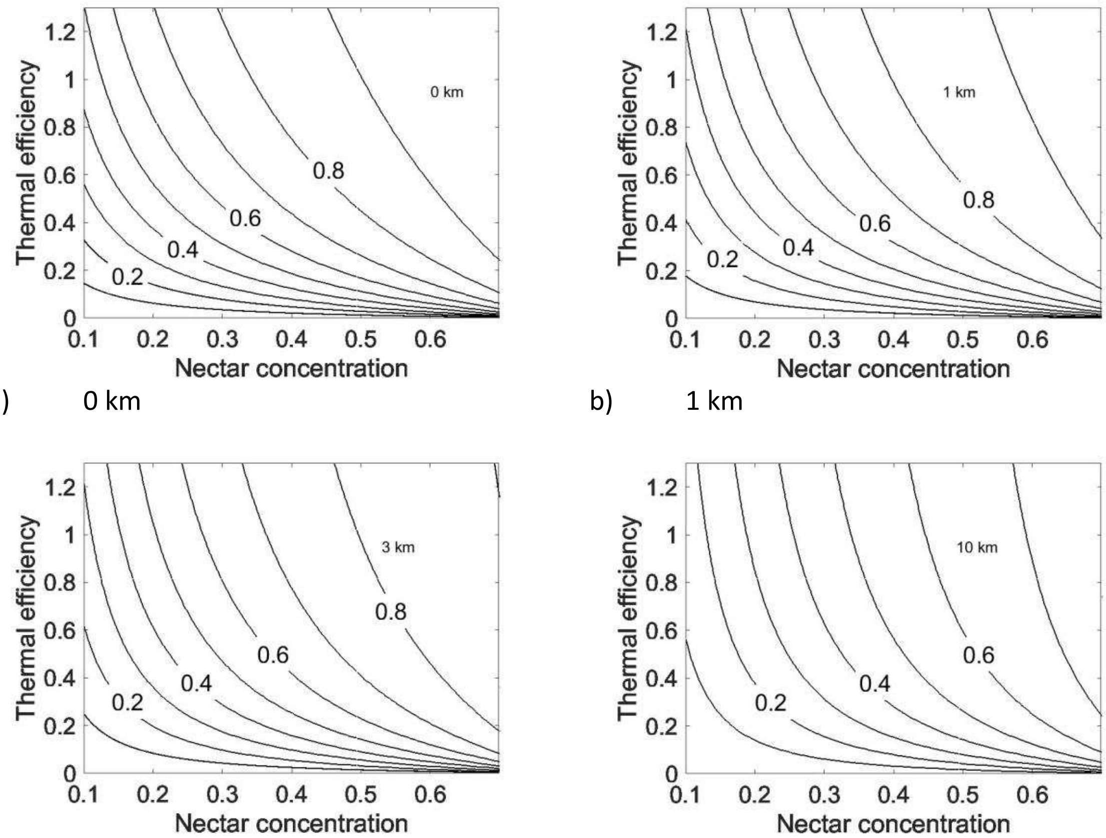


Fig 2: Collected nectar to honey factor contours vs nectar concentration and thermal efficiency for various distances(a-d)

From equation(39) we can determine the energy recovery ratio of the process of fetching the honey and processing the nectar into honey. This is shown in contour graphs for constant distance between nest and nectar source in Fig 3.



a) 0 km

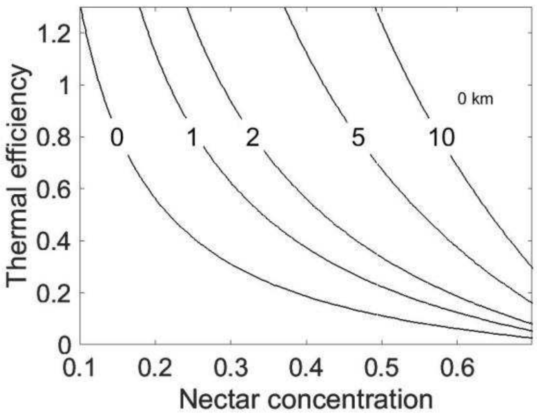
b) 1 km

c) 3 km

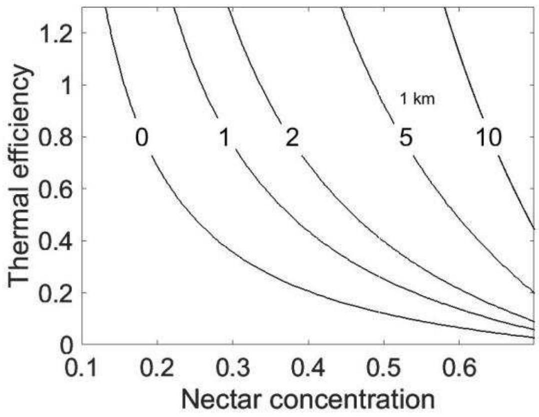
d) 10 km

Fig 3: Contours of energy recovery ratio vs nectar concentration and thermal efficiency

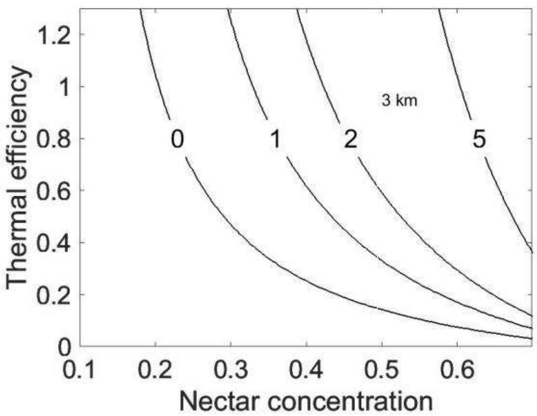
From equation (42) one can plot contours of HEM in Fig 4. Note this value is greater than zero when the energy is above break even.



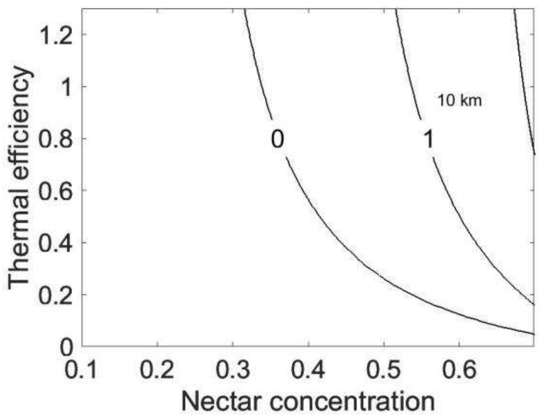
a) 0 km



b) 1 km



c) 3 km



d) 10 km

Fig 4: Honey energy margin contours vs nectar concentration and thermal efficiency at various distances to nectar (a-d)

From equation (43), the break-even point for foraging nectar for honey is shown in Fig 5. Derived from equation (40), Fig 6 gives the relative magnitude of the energy used in the process of honey ripening to that of energy delivered to the nest entrance.

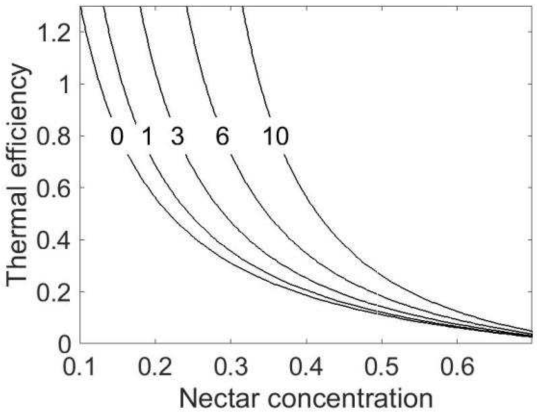


Fig 5: Contours of the break-even distance Km vs thermal efficiency and nectar concentration

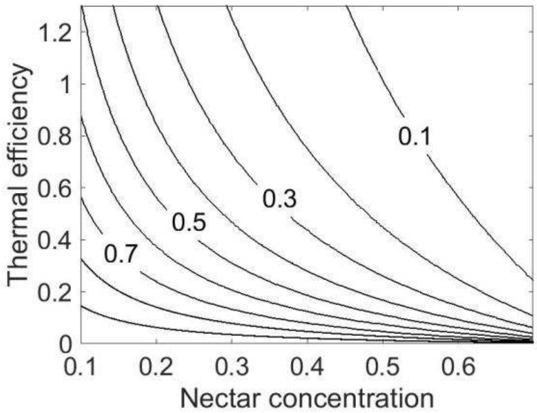


Fig 6: Contours of the fraction of delivered energy spent on nectar desiccation vs thermal efficiency and nectar concentration

6.3 Agreement with experimental data and observations

There are only isolated experimental data for the parameters that allow one to determine thermal efficiency i.e. honey ripening rate [45] and the nest lumped conductance [47]. The experimental lumped conductance values available do not take account of the contributions from nest internal structures, honey bee behaviours, seasonal variation or bee keepers adding boxes. However, there is sufficient data and dimensional parameters to determine valid ranges for these values. While it is clear that considerably more work is needed to add to the sparse data, there are experiments and data in the literature that are relevant to validating the model to some extent, as described in the following sections.

One of the results of the model presented here is that higher ambient temperature with a constant honey ripening rate would give rise to a higher TEE. Consequently, the honey bees would be able to profitably forage on lower concentrations of nectar (provided the RH was not raised as well). One study [14] has shown that by raising the external temperature of presumably a wooden hive in an internal apiary, the honey bees start collecting from flowers of lower nectar concentration; yet collect the same amount of sucrose by increasing the total number of flights, thus satisfying the models prediction.

Honeybee nectar foraging has been shown to extend beyond 9 km [61] in infrequent, particular circumstances. The exceptional 9 km foraging distance was recorded on a heather moor. Research has shown that, in the right circumstances, heather can yield up to 60% sugars [62]. This analysis shows the combination of 60% nectar concentration, a warm day of 25 C and wooden hives of conductance 2.6 WK^{-1} [47], would result in a TEE of 0.15 to 0.2 Fig 1. This TEE and nectar concentration would be within the break-even distance even at 9 km (Fig 5) where 25% of energy is being used for nectar desiccation (Fig 6). However, it also shows that if the majority of the nectar sources are in the range of 20% to 30%, then we would expect most nectar foraging to be under 5km, which concurs with other studies in heather [63,64] and those that include oil seed rape in Northern Europe.

In the models above, decreases in hive thermal conductance give rise to an improvement in thermal efficiency, which in turn gives rise to an improvement in HEM (Fig 4), which allows more nectar to be desiccated to honey. Thus one would expect from the analysis that decreases in hive conductance improve honey yields. This has been shown to occur in practice, in both formal studies [65] and anecdotally, to give increases of up to 30% in yield [66] . The latter were from expanded polystyrene hives. These have been measured at 1 WK^{-1} compared to 2.6 WK^{-1} for wooden hives and 0.4 WK^{-1} for tree nests [47]. The graphs in Fig 1 combined with the conductance values from reference [47] show the improvement in thermal efficiency of expanded polystyrene hives compared to the common thin walled wooden hives.

As the temperature of the desiccating air is increased, its water carrying capacity (the mass of water/ unit mass of air at saturation) is increased [67]. Thus less air needs to be moved to remove the same mass of liquid water. This temperature increase therefore improves TEE. If TEE was an evolutionary driver of honey bee behaviour, we may expect the nectar desiccation process to take place in a part of the hive where it takes less energy to maintain a higher temperature. This is shown by honey bees preferentially depositing nectar in the upper portions of their nest i.e. above the brood nest [68]. The temperature stratification above the heat source [47] of the temperature controlled brood area, reduces the heat requirements and air movement energy for honey production. The insulating properties of empty comb [69] enable losses to be reduced away from the walls of the nest which aligns with the observed behaviour of depositing nectar on combs not facing the outside walls [68].

The requirement to retain elevated temperatures, and hence reduced RH where the desiccation is taking place, shows an all year round advantage for nests with low thermal conductance. This would drive honey bees to seek out such nest sites i.e. tree hollows rather than ground crevices, with lower thermal conductance values (thick wooden walls, bottom entrances)[70,71] and modify, where possible, nest sites to further reduce the conductance value by for example closing up holes with propolis.

7 Discussion

7.1 Nectar desiccation energy significance

In Fig 6, at a TEE of 1.0, one can see that for a Northern European oil seed rape crop of 30% nectar sugars [64], the nectar desiccation process consumes 25% of the energy in the nectar delivered to the entrance. Similarly on clover with 20% [72] sugars, it will consume 40% of the delivered energy .

At a TEE of 0.4, the situation is even more pronounced; desiccation consumption rises to 40% and 60% for rape and clover respectively. Thus one can clearly see, that the process of nectar desiccation into honey is a significant proportion of the energy collected, and that TEE, and consequently nest lumped thermal conductance are significant factors in the energy collection of *A.melllifera*.

7.2 Behaviour, lumped thermal conductance and TEE.

TEE as seen in equation (21) is a function of: honey ripening rate, which one expects honey bees to maximise; nectar concentration, which the honey bees try to maximise from what is available [73,74]☐☐; ambient temperature, which is out of the honey bees control, and finally the lumped thermal conductance. This is formed from a series network which includes the advective heat transfer of the internal air to the nest wall (equation (22)). This is dependent on the air flow across the internal and external surfaces (equation 23) and therefore on the behaviours of the honey bee colony, and consequently so is the TEE. Armed with this knowledge, researchers can now interpret and quantify the benefit or other wise of the details of fanning behaviour internal to the nest in conjunction with external factors, such as temperature and available nectar. For example, if behaviours were found that directed the air heated by honey bees, so that it is kept away from the walls of the nest until after it was laden with water vapour, this would dramatically reduce the lumped conductance and increase TEE.

7.3 Extended distance and variety

From inspection of Fig 5, it is evident that an increase in TEE from perhaps an increase in the ambient temperature or a behaviourally lowered lumped nest conductance, allows the honey bees to profitably retrieve nectar and refine to honey from either a weaker nectar source or from a greater distance. For example: at a concentration of 30% (0.3), an increase in TEE of 0.4 to 0.6 increases the break-even range from 1 Km to 5 Km. Similarly, at a range of 1 Km, an increase in TEE from 0.3 to 0.6 enables a decrease in sugar concentration from 32% to 20% to be equally profitable in honey. A colony that collects nectar at distances, concentrations and TEE outside the break-even line will not add to its honey reserves and risks extinction e.g. collecting 25% concentration at TEE of 0.5 at distance of 5 Km. ☐

7.4 Improved TEE reduces wing wear

Efficient usage of the limited wing lifetime of honey bees has been shown to be an important factor in colony success [41,75,76]. This analysis has shown (Fig 2), for the same amount of honey, improvements in TEE require less nectar and hence less foraging flights resulting in less flight wing beats and consequently less wing wear.

Further, improved efficiency in evaporation reduces the total amount of water that needs to be both evaporated and moved by fanning and hence reduces the wing beats and the wing damage that occurs from fanning activity [49].

7.5 Decreased thermal conductance increases profitability

Improved TEE results in more energy being stored as honey, and therefore increased honey yields for a given colony size and forage area, which not only improves the chances of survival, but it can also improve the revenue for commercial honey bee farmers. This analysis points the way for bee farmers to increase yield and revenue by working synergistically with their honey bees to improve thermal efficiency by changing their hives to ones which lose less heat, and facilitating honey bee behaviours that have the same goal e.g. bottom entrances.

8 Conclusions

Honey bees are bound by the physics of water evaporation. In exploring the physics we can see that nectar desiccation is a substantial part of the work done inside a honey bee nest even in the most favourable circumstances. The relations uncovered in this research have quantified those boundaries and have been validated by experimental work, but only as far as the current very sparse data allows. The magnitude of the energies devoted to nectar desiccation show this area is worthy of more experimental research and detailed analysis.

The relations found show that:

- Desiccation of honey takes a significant percentage of the energy delivered to the hive in the form of nectar for *A.mellifera,* particularly in the northern part of their range where nectar is lower in concentration. Typical values show that over 50% of the delivered energy may be used in the process of honey ripening and even in exceptionally favourable circumstances for temperate climates, do not use less than 25%.
- The relative magnitude of the energies involved and the ratios of nectar to honey show that thermal energy efficiency of nectar desiccation should be considered as a key factor in the development and success or otherwise of honey bees in temperate climates where nectar sources are widely dispersed and of lower concentration.
- The lumped thermal conductance of hives, previously thought to be only a consideration for winter, has been shown to be a major factor during the nectar collecting periods of the year and is dependent on honey bee behaviour.
- The energy consumption of nectar desiccation and hence TEE, limits the maximum foraging distance of honey bees. It also changes the energy return for a given nectar source and a consequence which nectar sources are viable for the honey bee.

This appreciation of the importance of TEE improves our understanding of why honey bees moved into tree cavities and provides background into why they have developed their behaviours. It provides a new avenue for the research of honey bee behaviours and a firm theoretical foundation for improving the survival of colonies in the face of climate change and improving the honey yield for bee keepers by reducing the values of hive thermal conductance to be closer to those found in tree nests. Further work is required to investigate how honey bees interact with the bounds described by the models and expanding their scope to take account of the 3 dimensional heat and air flows within the nest.

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10 Competing interests

The author has no competing interests.

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