FUTURISTIC BEEHIVES FOR A SMART METROPOLIS

Deliverable D5.2

Models and simulations of population dynamics

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Introduction

Purpose and scope of the document

In this deliverable, we describe in detail the HIVEOPOLIS models for in-hive population dynamics (task 5.6). The models focus on brood development and predict the number of newly emerging adults. We report how temperature data from a sensor/actuator comb is used to estimate the amount and age distribution of brood currently present in a hive. We provide evidence that this approach is actually working and allows us to estimate the number of newly produced workers. This information can then be fed into the HIVEOPOLIS Core-model where it will be - together with data from other modules (e.g. on foraging activity, weather, food availability, etc.) - used to describe and predict the overall colony performance.

Overview of the document

We start this document with an overview of thermoregulation in honeybee colonies and a simple model of colony weight (Chapter 1). We then describe a spatially explicit model, which simulates the brood nest development on one side of a brood comb, mimicking the features of our sensor/actuator combs (Chapter 2). We use this model to explore how we can predict the amount and age-distribution of the brood with the "Brood Estimator Tool" and show that we can actually estimate the real brood nest size of an experimental colony, based on the temperature data (Chapter 3). Finally, we describe how this information about the brood nest can be fed into the HIVEOPOLIS Core-model, where it will affect the overall colony performance.

1. Honeybee thermoregulation and a simple model

1.1. Thermoregulation of the colony

Honey bees as social insects are very good at thermoregulation - they can regulate temperature inside the hive, specifically in the brood nest area where it is crucial to keep the temperature between 32 °C and 36 °C to ensure proper development of new bees (starting from larvae and pupae stage) (Seeley & Heinrich, 1981; Tautz et al., 2003; Becher et al., 2010; Stabentheiner et al., 2010). To control the temperature bees perform: (1) fanning operations to ventilate the hive or perform evaporative cooling (in case it is too hot); (2) heating operations (during winter a cluster is formed) (Jarimi et al., 2020). However, temperature in the bee hive is not evenly distributed (mainly to avoid wasting energy) - in the brood nest area (and inside the bee cluster during winter) it is higher and changes less than the temperature near the hive walls. Thus bee colony temperature monitoring can provide valuable information concerning the bee colony status, behaviour and potential problems.

Nowadays, bee colony temperature measurements seem to be the simplest and cheapest way to monitor bee colonies. There are a lot of studies (Seeley et al., 2003; Stalidzans & Berzonis, 2013; Kridi et al., 2014; Meikle & Holst, 2015; Gil-Lebrero et al., 2017) and practical experiments involving temperature measurements of bee colonies and many scientists tried to understand the bee behavior features depending on environmental parameters. The low costs of data collection, processing and data transfer of temperature measurement systems facilitate application of temperature measurements in beekeeping.

Based on temperature information, it is possible to detect different colony states such as increased food consumption, the start of brood rearing, swarming states, and colony decline resulting in death of the bee colony. Brood volume and winter cluster volume can also be identified by monitoring colony temperature (Zacepins et al., 2015). To determine brood volume, many sensors (one or even two per frame) should be placed into the hive. Another approach is to use a single sensor, placing it above the upper hive body in the middle of a horizontal cross section, increasing convenience and reducing costs. In this case data analysis and decision support become more challenging. In any case, a direct influence of ambient temperature on the measurements has to be assessed.

For the practical beekeeper, placing many sensors in the colony is not very convenient, thus bee colony monitoring with one sensor is more preferable. There is some evidence that even with one temperature sensor some valuable information can be collected from the continuous measurements (Ferrari et al., 2008; Stalidzans & Berzonis, 2013; Kridi et al., 2014; Zacepins et al., 2015; Kviesis et al., 2020). It is clear that a precise evaluation of the amount of brood in the colony is not possible, but the transition of the colony from passive (wintering period, when there are no brood rearing activity) to the start of the brood rearing process and active rearing states is possible. As it was mentioned before, during the intensive brood rearing period honey bee colonies maintain a stable brood temperature (32 °C - 36 °C), where temperature values up to 35 °C can be detected above the frames with only one temperature sensor.

In general, several stages can be distinguished describing the annual bee colony development (Stalidzans & Berzonis, 2013):

- winter brood rearing (8 ℃ < T < 17 ℃);
- spring brood rearing (17 ℃ < T < 33 ℃);
- summer brood rearing (33 ℃ < T < 36 ℃);
- autumn brood rearing (33 ℃ > T > 17 ℃);
- autumn broodless period (17 ℃ > T > 8 ℃);

Below several images are presented to demonstrate the temperature dynamics in the colony measured by one sensor (placed above brood frames). Fig. 1.1 demonstrates the change from passive state to the brood rearing state. It can be observed that colonies can start the brood rearing process at different times.

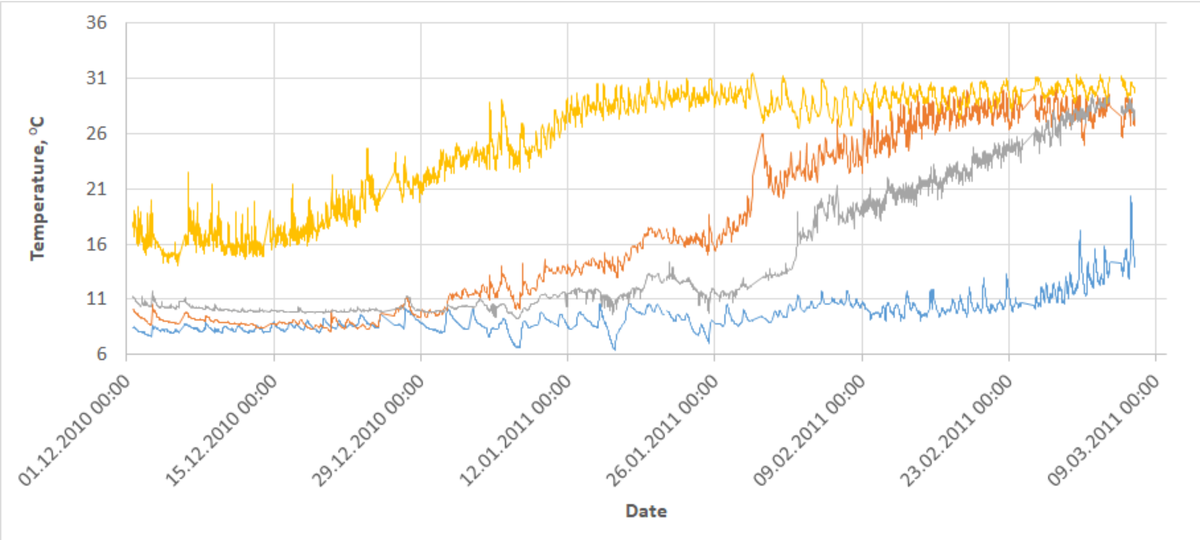

Fig. 1.1: Example of temperature changes during start of the brood rearing process. Lines represents temperature inside the hives (above brood frames)

Schematic visualisation of the bee colony active brood rearing state is demonstrated in the Figure 1.2 below:

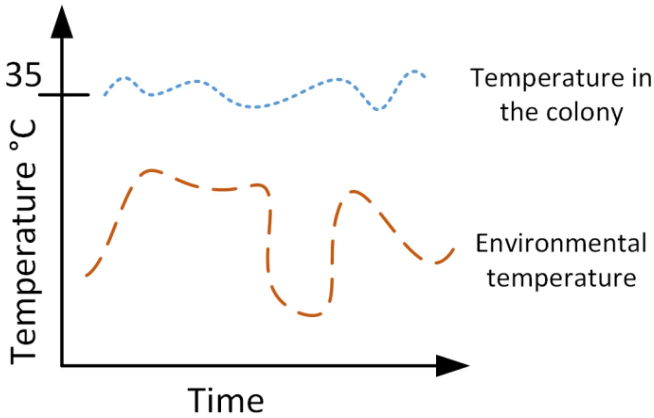

Fig. 1.2 Schematic visualisation of the bee colony active brood rearing state

During early summer, the temperature is kept quite stable (see Fig. 1.3) and is not affected by the changes in ambient air temperature. This can be explained by the fact that the colony should maintain a stable high temperature for the brood.

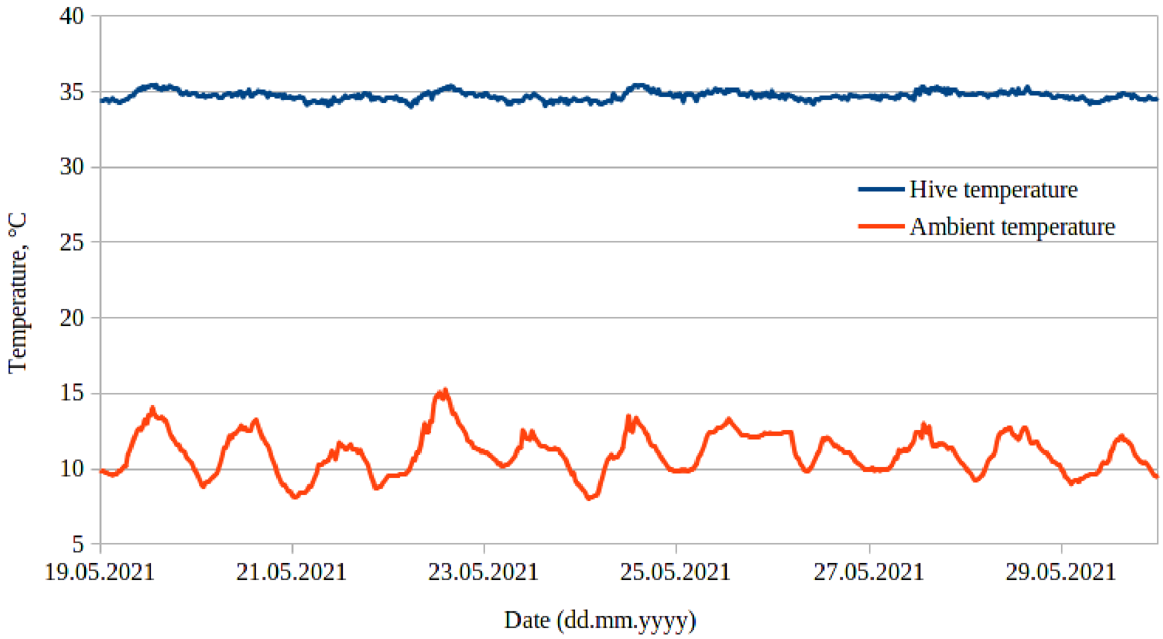

Fig. 1.3: Example of temperature values (°C) during the early start of summer (end of May). Blue line - temperature inside the hive (above brood frames), red line - ambient air temperature

The temperature above the brood frames during the winter period is well below 20 °C (see Fig. 1.4) and could be a good indicator of whether the colony has started an early active brood rearing process, or of whether it has a disease (e.g., nosema) that can cause the rise of temperature.

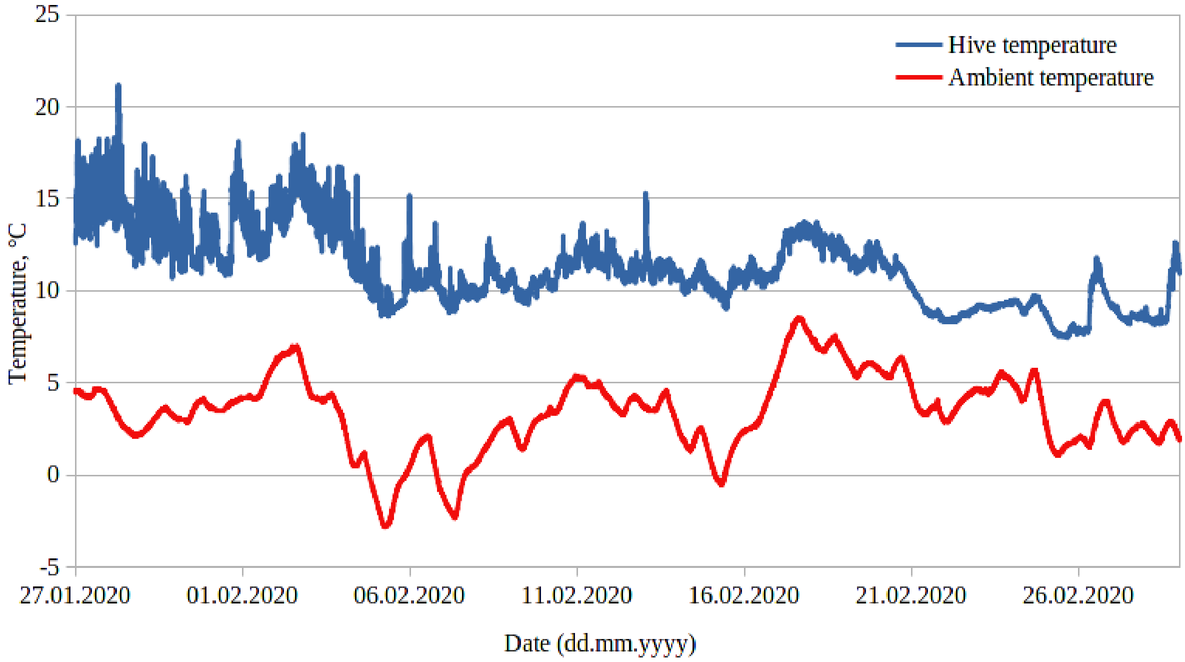

Fig. 1.4: Example of temperature values (°C) during the winter period (end of Jan. - Feb., 2020). Blue line - temperature inside the hive (above brood frames), red line - ambient air temperature

Brood rearing detection and evaluation is important as it can help to identify the strength and development stage of the colony. Sometimes an early start of the brood rearing is unworthy, for instance, if a colony starts to actively make brood during the winter, colony food resources can come to an end before the start of the foraging season. To have an impact on the brood rearing process, it is possible to heat/cool down the brood frames.

These examples show that placing one temperature sensor inside the hive can provide a general overview of the honey bee colony, but sophisticated models are needed to get more insights and a better understanding of the bee colony dynamics and development process.

1.2. Limited number of variables models

In an operational perspective, where monitoring key indicators is essential, it is important to not only search for adequate variables to follow but also to have a global view of what could be the outcome for given environmental parameters and initial conditions. The advantage of mathematical models with a limited number of variables and parameters is to have analytical expressions to be able to quickly make predictions without too much computational power. In these settings, the laws governing the dynamics are expressed in terms of functions that account for global processes, rather than for particular individual behaviours, that may be difficult to monitor. Although relatively simple in their shape, these “simple models” can predict complex global behaviours in a straightforward fashion.

In our quest for the simplest variable to monitor that is a good indicator of the health of a hive, the total weight of a beehive seems to be a good choice (Hambleton, 1925; Meikle & Holst, 2015; Meikle et al., 2018). We developed a general model of the time evolution of the weight. It accounts for a positive term, expressing the growth of the weight due to cooperative processes such as birth, nursing and food foraging, and a negative term, expressing food decay through food consumption and death rates (constant and due to lack of food). The model can be written as

$$\frac{dq}{dt} = \alpha\frac{q^n}{q^n+k_1^n} - \left(\mu_1 + \frac{\mu_2}{\frac{q^m}{k_2^m}+1}\right)q \qquad (1)$$

were α is a parameter combining environmental factors such as the food availability, temperature, etc. k_1 is the threshold weight from which the growth is effective and n is the strength of cooperative processes leading to the growth. In the negative term, μ_1 represents the constant linear disappearance rate due to consumption and death and μ_2 represents the maximal death rate due to lack of food. As for k_2 and m, they account for the amount of weight from which the situation becomes critical and for the steepness of the decay. In the sequel, for analytical accessibility, we will choose as parameter values $n = m = 2$.

Although a real beehive is never at equilibrium, it is however informative to solve eq. (1) at the steady state. Putting $\frac{dq}{dt} = 0$ yields

$$q\times\left(-\mu_1q^4 + \alpha q^3 - \left(k_1^2\mu_1 + k_2^2\mu_1 + \mu_2\right)q^2 + k_2^2\alpha q - \left(k_1^2k_2^2\mu_1 + k_1^2\mu_2\right)\right) = 0 \qquad (2)$$

Looking at eq. (2), one notices that the solution $q = 0$ always exists and that a maximum of four other solutions may be present. However, solving the quartic equation always led to two (one stable and one unstable) real positive solutions along with the trivial solution $q = 0$. Figure 1.5 displays the bifurcation diagram of the steady state of q as a function of the parameter α. It shows the existence of a critical value of the parameter α below which the beehive collapses (weight $q = 0$), in agreement with the literature (Seeley & Visscher, 1985). Beyond this critical value, the beehive may or may not grow depending on its initial condition and on the randomness of the environment. In other words, if the system is above the unstable branch, the beehive will gain weight and reach the above stable branch, otherwise, it will collapse.

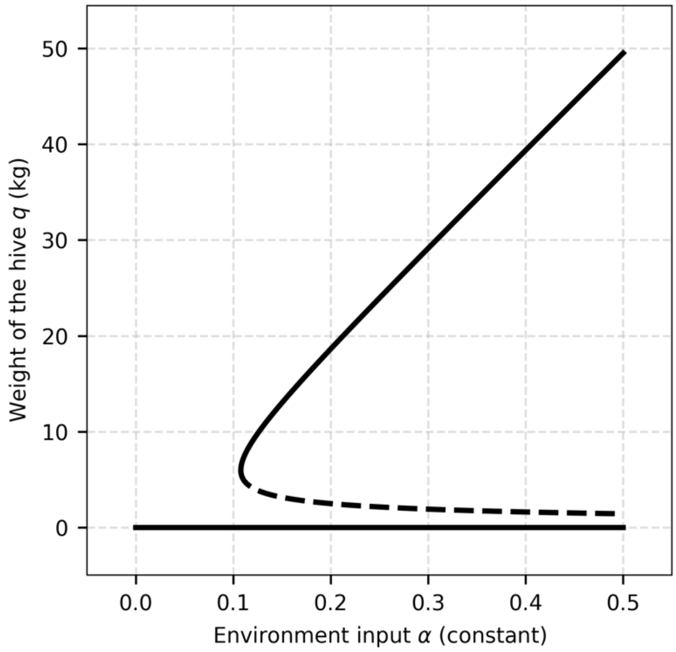

Fig. 1.5: Bifurcation diagram of the steady-state solutions (eq. (2) as a function of the parameter α. Parameter values are $k_1 = 4$, $k_2 = 2$, $\mu_1 = 0.01$ and $\mu_2 = 0.09$.

It is important to note that beyond the critical value of α where the bifurcation point appears, as α is increasing, the attraction basin of the trivial solution is shrinking, signalling that the probability of the beehive to collapse is decreasing.

As said earlier, a beehive is never reaching some sort of a steady state. It is subjected to external forces such as food availability, which is itself dependent on the seasons, and on the external temperature. In these settings, the parameter α becomes time-dependent, $\alpha(t)$, and can be seen as an input signal monitored. For the sake of simplicity, the input signal is taken to be binary, being equal to zero from January to end of April and from September to end of December, and equal to a constant value α_{max} from May to the end of August (black dotted line in Fig. 2a).

$$\alpha(t) = \{0 \ if \ Jan < t < May \, or \, Sep < t < Dec \, and \ \alpha_{max} \ if \ May < t < Sep \tag{3}$$

Integrating the model for several years with this time-dependent input leads, depending on the initial conditions, to entrained weight oscillations which can eventually collapse very quickly or last for some time (Fig. 1.6a). Fig. 1.6b shows for three different values of α_{max} the number of years it takes for a beehive to collapse as a function of its initial condition. One notice that small changes on the initial weight or on the maximal input can lead to the gain of several survival years.

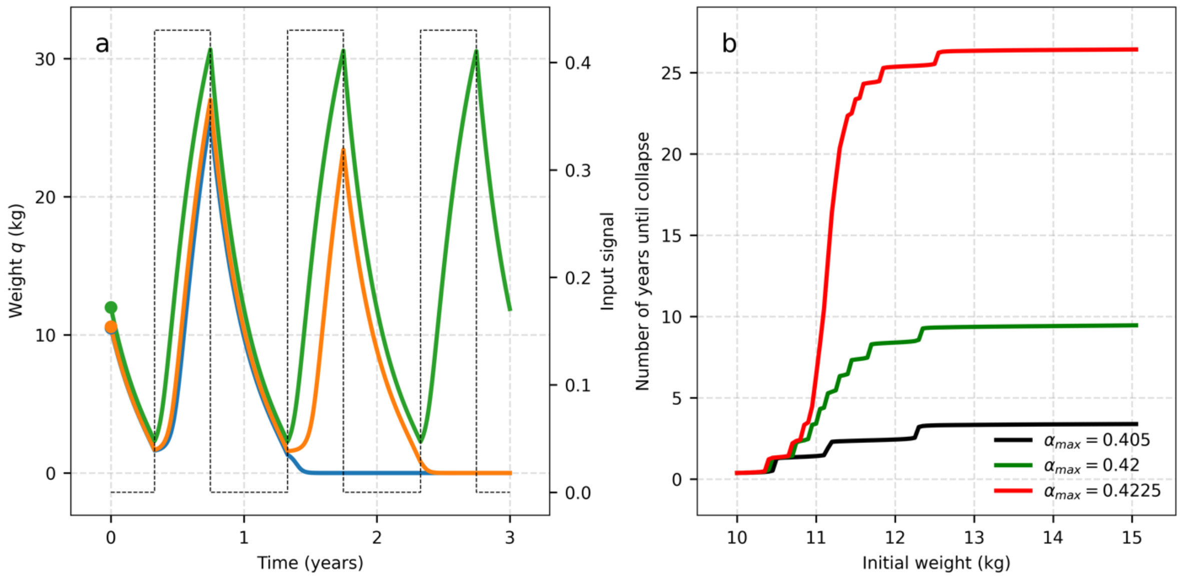

Fig. 1.6: Numerical integrations of eq.(1) where α is replaced by the time dependent relation of eq. (3). (a) Three different trajectories starting with three different initial conditions ($q_0 = 10.5$kg (blue line), $q_0 = 10.6$kg (orange line) and $q_0 = 12$kg (green line)). $\alpha(t)$ is drawn in black dotted line and $\alpha_{max} = 0.42$. (b) Number of years it takes for a hive to collapse ($q < 1$kg) as a function of its initial weight for three different values of α_{max}. Other parameter values as in Fig. 1.6

A more general view is provided in Fig. 1.8. where the number of years needed for a hive to collapse against its initial weight and the maximal environment input α_{max}. As seen, below an initial weight, the hive collapses before the first year, whatever the value of α_{max} is. This region is however decreasing when increasing α_{max}. Beyond this value and for a small α_{max} the hive is able to survive for 3 to 6 years. At a critical value of α_{max} (around 0.425), when increasing the initial weight, the hive, the life expectancy increases until 27 years. Beyond this critical value, and given a sufficient initial weight, the hive becomes immortal (white region of Fig. 1.7).

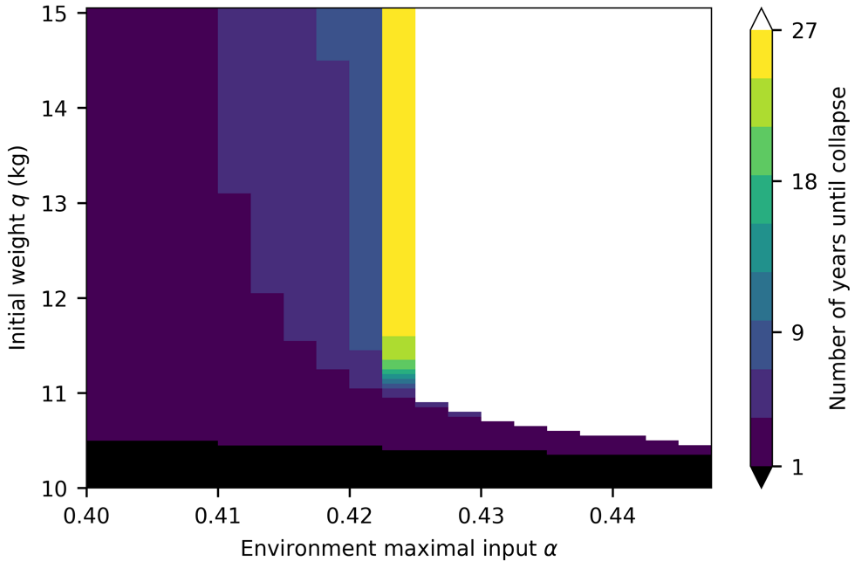

Fig. 1.7: Number of years until a hive collapses as a function of its initial weight and of the environment maximal input α_{max} as given by the numerical integration of eq. (1) and the signal given by eq. (3). The white region corresponds to the situation where the hive never collapses. Other parameter values as in Fig. 1.6.

We now augment the mean-field description by carrying out Monte Carlo type simulations. We still take a deterministic input given by eq. (3), but we put the stochasticity on the increase of the weight while the loss is deterministic. Figs. 1.8a, b show the probability distributions of the weight for the three first years and for two different initial conditions ($q_0 = 12$kg (a) and $q_0 = 15$kg (b)). As shown, for the smaller initial condition, a small proportion of realizations ends up with the collapse of the hive. This proportion increases significatively in the second and third year. As for the larger initial condition, all the realizations ended up with the survival of the hive and it is only during the second year that 1/5 of the realizations collapsed. Figs 1.8c and d show the corresponding mean and standard deviation (including and excluding collapses) weight through 3 years' time from these different initial conditions. We see that the weight is entrained by the time-dependent signal but also that the oscillations are damped as time increases, signaling, for these parameters and initial condition values, that the hive will eventually collapse.

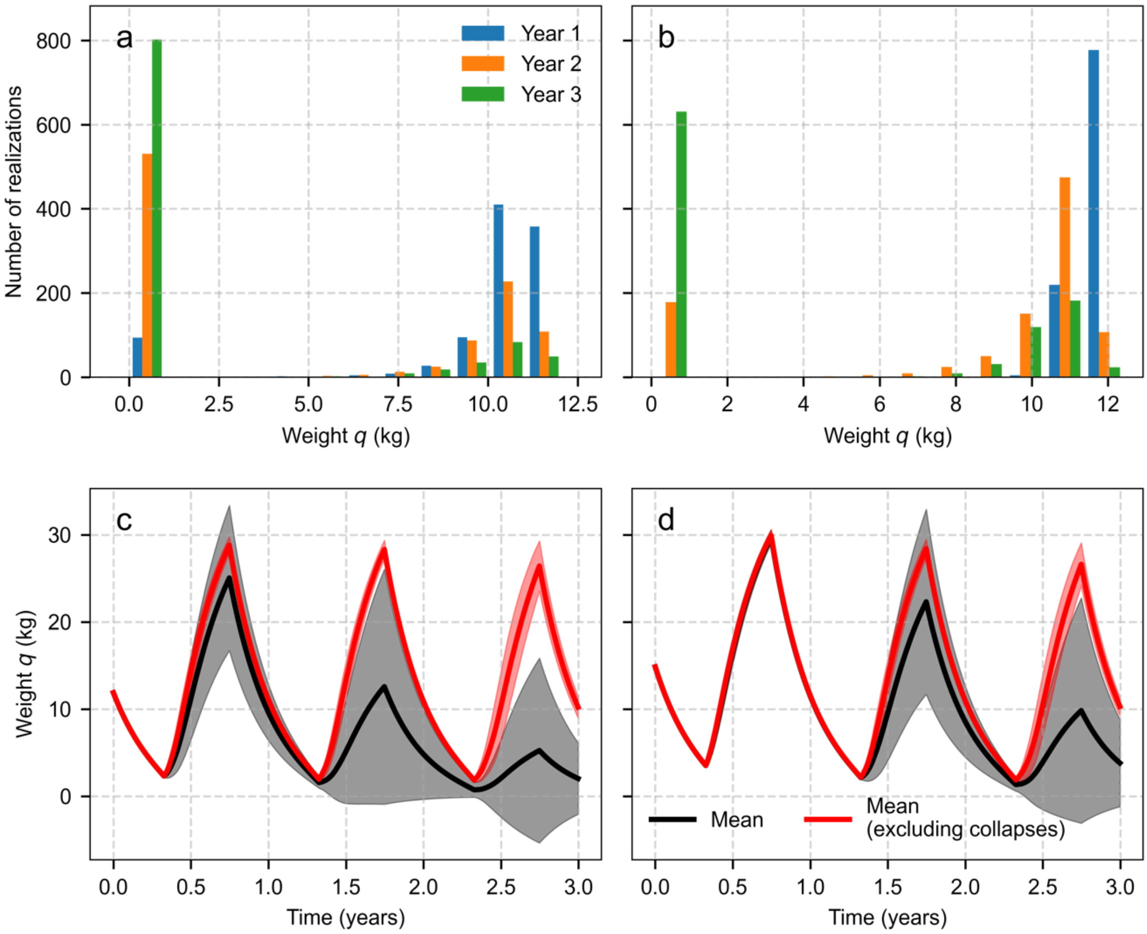

Fig. 1.8: Probability histograms of the weight (a and b) and time evolution of the mean and standard deviation weight (c and d) as the result of 1000 Monte-Carlo realizations ran for 3 years (3 times 365 days). Initial conditions are $q_0 = 12\text{kg}$ (a, c) and $q_0 = 15\text{kg}$ (b and d) and $\alpha_{max} = 0.4$. Other parameter values as in Fig. 1.5.

Finally, Fig. 1.9 shows the probability to collapse as a function of time for two different initial conditions and two different α_{max}. Again, they show how small differences can result in a better life expectancy of the hive.

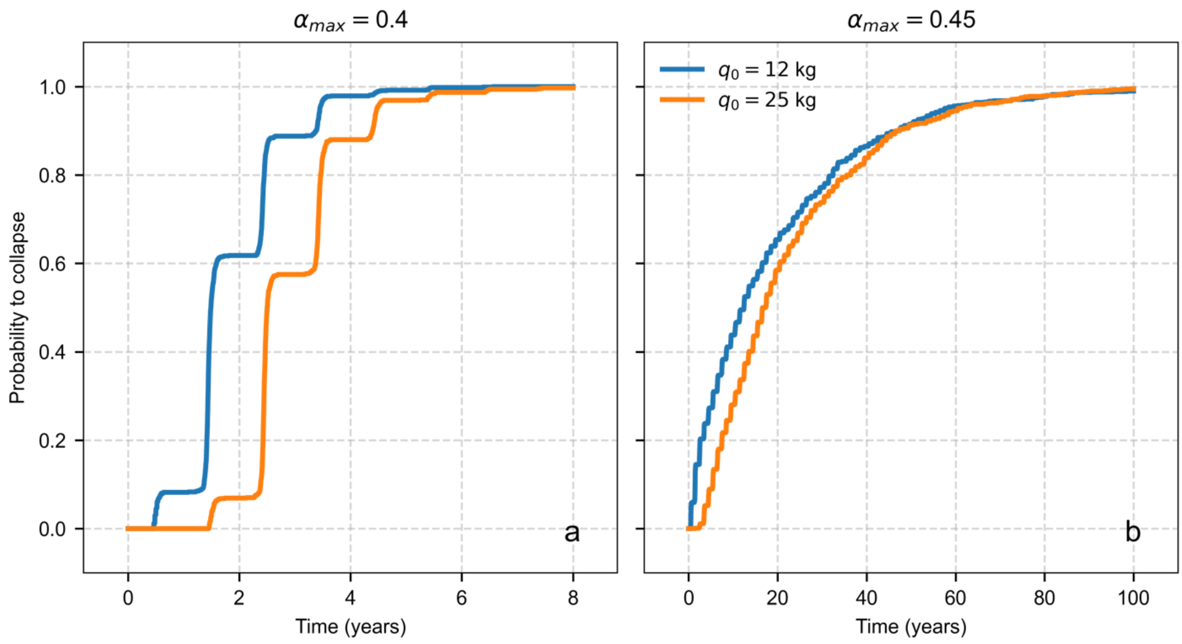

Fig. 1.9: Probability for a hive to collapse as a function of time as a result from 1000 Monte Carlo realizations. Other parameter values as in Fig. 1.5.

2. Simulation of brood nest patterns

2.1. Objectives of the Brood Nest Model

We developed a spatially explicit model that simulates brood nest and temperature patterns on a single sided comb.

With this model, we had the following objectives in mind:

1) Improvement of our understanding of the system

The model helps us to study how a compact brood nest can be formed in a self-organised way based on a few, simple behavioural rules regarding the movement and heating activities of the bees.

2) Guiding the engineering of the brood nest module and experiments

The model mimics our Sensor/Actuator combs. This allows us to simulate experiments in advance in order to optimise their setup. The model can also help to improve the design of future Sensor/Actuator combs, e.g. by testing how a change in the number of temperature sensors or heat pads may affect the quality of our data or the response of the bees.

3) Visualisation and interpretation of experimental data

The model can also be used to visualise and interpret experimental data, especially regarding the temperature gradient and brood nest size. This leads to the development of the Brood-Estimator Tool (Chapter 3).

2.2. Model Description

The Brood Nest Model was developed in Netlogo 6.2 (Wilensky 1999) which is freely available at https://ccl.northwestern.edu/netlogo/

2.2.1 Elements

The comb

The model represents one side of a single honeybee comb. For reasons of simplicity, we implemented the comb as a 2-dimensional lattice model with rectangular cells instead of a more realistic pattern with hexagonal cells. The differences between these two approaches are small and the impact on the results should be - if at all - minute. The dimensions of the comb are variable, but reflect under default settings the dimensions of the Sensor/Actuator

Combs (**see chapter 3.2 Sensor/Actuator combs**), i.e. 78 x 39 cells. The comb is implemented via the NetLogo "World" feature.

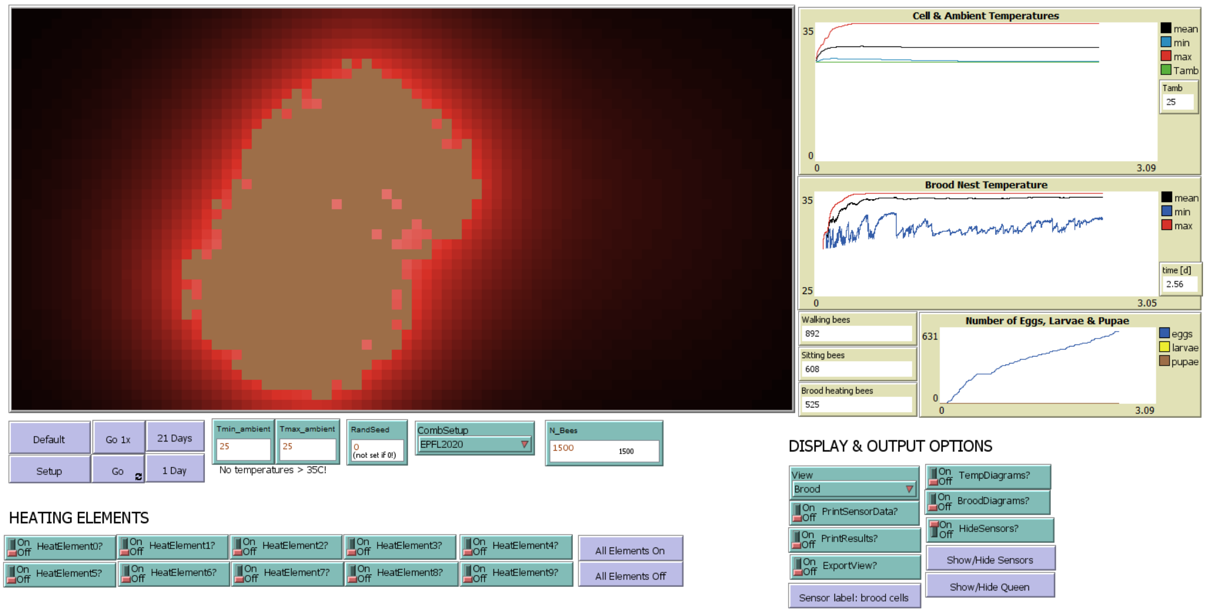

Fig. 2.1: Screenshot (cropped) of the interface of the Brood Nest Model. The main image shows one side of a comb, with brown cells being brood and black to red cells visualising the temperature gradient of empty cells. Worker bees and the queen are hidden.

The cells

Cells are either empty or they can contain brood. Honey and pollen stores are not considered in this model at all. Each cell has a certain temperature which is reset in every time step, depending on the temperature flow on the comb. There can not be more than one adult bee sitting on a cell (for an extended period of time) and one or more bees can walk over it during a single time step. The cells are implemented via NetLogo "patches".

The queen

The queen is implemented as an agent, moving over the comb to lay eggs in suitable cells. Her movement follows to some degree a temperature gradient, produced by the heating activities of the worker bees. In order to be suitable for egg laying, a cell must be empty and has to have a temperature that is equal or higher than the queen's threshold temperature for egg laying. This threshold temperature of the queen is between 29.5 °C and 34 °C. If the queen lays an egg, the threshold temperature is increased, if she does not lay an egg, it is slightly decreased. I.e. the more time has passed since the last egg laying event, the lower the temperature of the cell can be to be acceptable for laying an egg. The minimal value of this parameter has to be below the temperature worker bees are aiming for when heating an empty cell, otherwise, egg laying would never be initiated.

Worker bees

Worker bees are either sitting or walking. In both cases, they are, at any given time step, associated with a certain cell (a Netlogo *patch*). There can never be more than one sitting bee per cell, whereas the number of walking bees per cell is not limited. This is to keep the model simple and to avoid a situation where a bee cannot move anymore when all neighbouring cells are occupied. In reality, bees will usually be able to squeeze through a group of bees or they just walk over each other.

The number of workers is set at the beginning and kept constant throughout a simulation run, i.e. there is no mortality among adult workers, no progression to foraging and no change in numbers due to newly emerged bees.

Workers perform a single task in the model, which is heating the cell they are on. This task is done by sitting bees, which try to raise the temperature of a cell to 30 °C, if it is empty, or to 35 °C, if it contains brood. Cooling of cells by the bees is not considered in the model. How bees move over the comb is described in 2.2.2 (Processes).

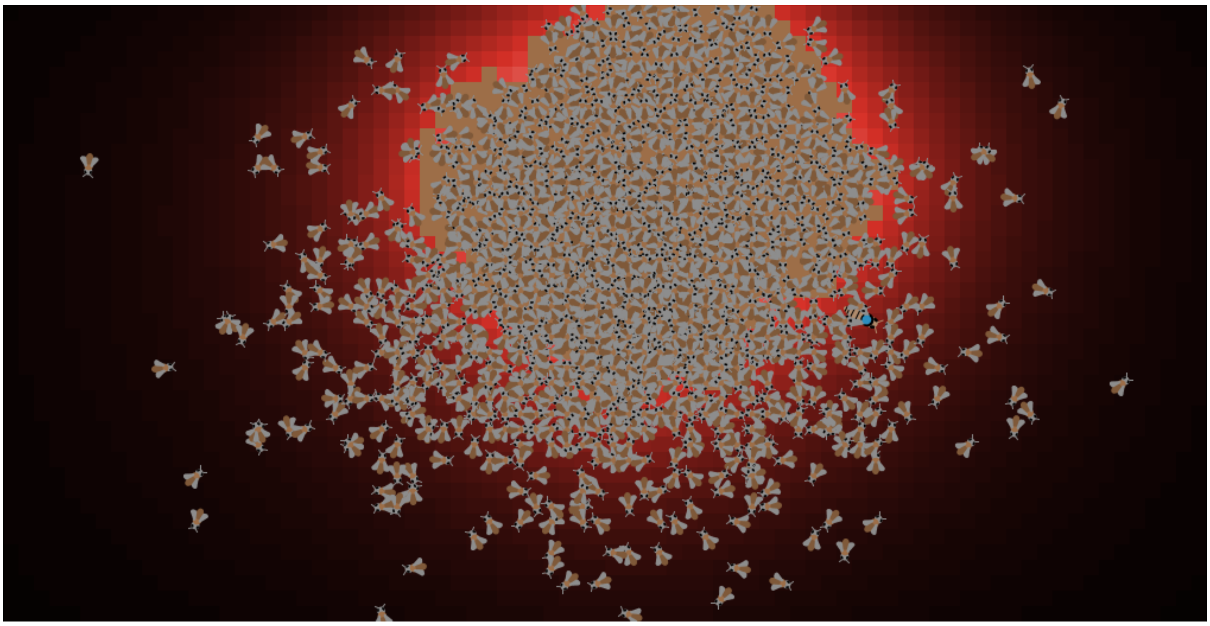

Fig. 2.2: The 1500 worker bees present under default conditions accumulate over the brood nest to heat it. The queen is shown as a larger bee with a blue tag on the thorax.

Brood

(Implemented via NetLogo "patches")

As soon as the queen lays an egg in a cell, this cell is considered as containing brood and the age of the brood is kept track of. Based on the age of the brood, its developmental stage is determined, with transitions from egg to larva, larva to pupa and pupa to adult taking place at specific ages. As the model focuses on brood nest patterns and is not a full-fledged colony model, the newly emerged bees disappear and the total number of workers in the simulation remains constant. (This could reflect a situation where in-hive bees develop into foragers, which do no longer care for the brood, at the same rate as new workers hatch).

Temperature sensors

To be able to compare real and simulated temperature distributions on the comb, virtual temperature sensors can be created, which are implemented as Netlogo *turtles*. Under default setting, a grid of 5 x 11 sensors is set up. Each sensor records the temperature of its associated cell with a certain frequency (default: every 10 minutes) and saves the recordings for 24 hours. When displaying the sensors on the interface, they can be used to plot their temperature and the amount of brood on their associated cells over the past 24 hours.

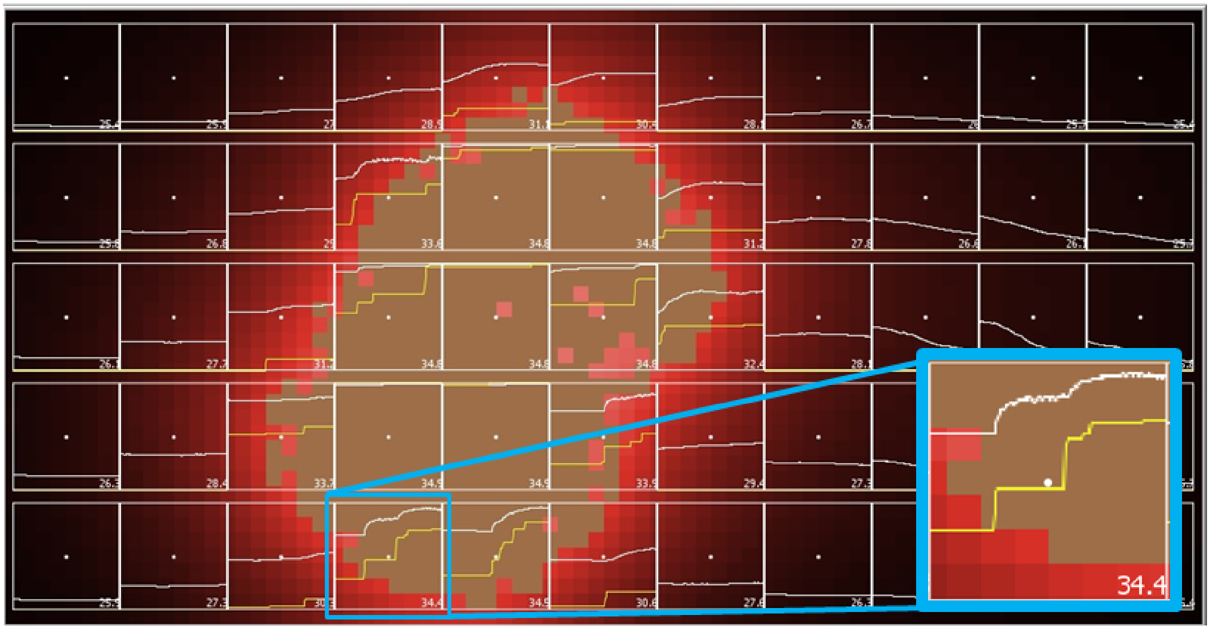

Fig. 2.3: Comb area with the sensor grid being displayed. The insert on the bottom right corner zooms into sensor 48: The white line shows the temperature of this sensor over the past 24 hours, the yellow line shows the amount of brood present around this sensor.

Heat pads

In order to mimic the heating feature of our existing real Sensor/Actuator Combs, we implemented virtual heat pads in the model. Two rows with five heating elements each are defined (via NetLogo *patches*) and can be switched on or off independent of each other. The size of the heating elements automatically adjusts to the dimensions of the comb, covering the whole area, i.e. under default setting, one heating element measures 15 x 18 cells. If a heat pad is switched on, all of the cells in its area are immediately set to 35 °C and maintain this temperature, irrespective of ambient temperatures or the behaviour of the bees.

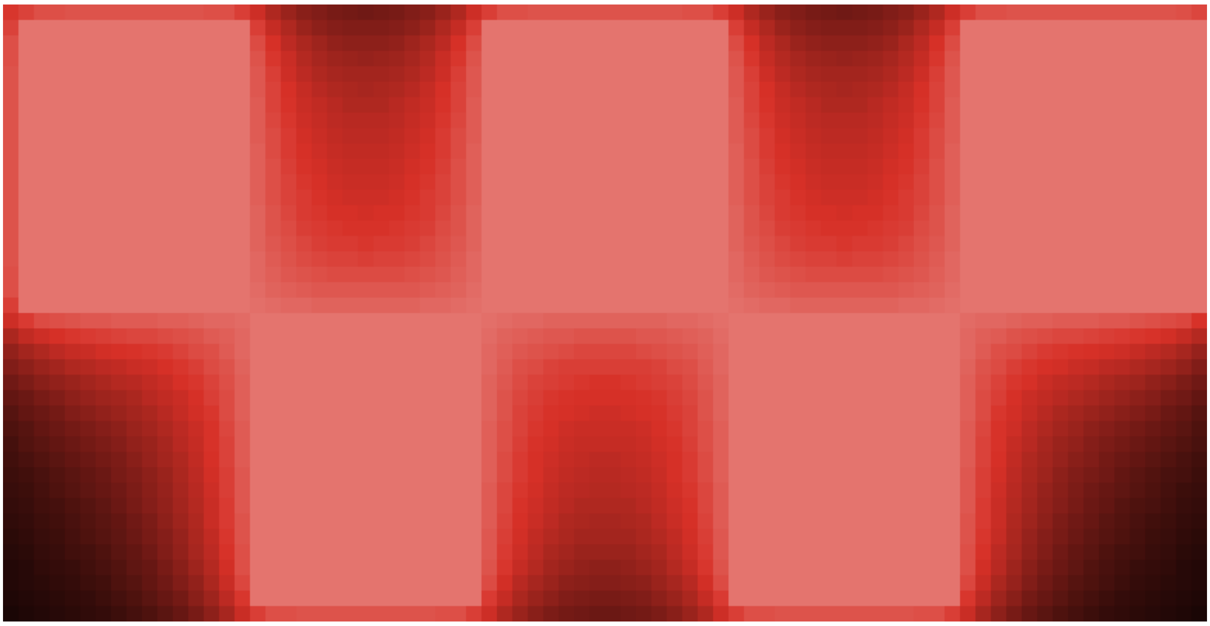

Fig. 2.4: Temperature distribution on the comb with five of ten heat pads being switched on (no brood present). The cells over the area of the heat pads have a constant temperature of 35 °C.

2.2.2 Processes

Movement of bees

During the setup, the adult worker bees are randomly distributed on the comb and defined as "sitting". In every time-step (5 s) they may start walking with a certain probability. This probability depends on the temperature at that location and the number of sitting bees in the immediate neighbourhood of a bee. Lower temperatures and fewer neighbours both increase the probability to move.

If a bee switches from sitting to walking (or already has been walking) they will move to one of the eight neighbour cells. With a certain probability, they follow the temperature gradient and move to the warmest neighbouring cell. If they do not follow the temperature gradient in this time step, the new cell is randomly chosen among the eight neighbours.

If a walking bee is then located on a cell where no sitting bee is already present, it may stop its movement and become a sitting bee. The probability to switch from moving to sitting is the complementary probability of switching from sitting to moving (e.g. if a sitting bee has a 25% probability to start moving, a moving bee would in the same situation have a 75% probability to stop).

Movement of the queen

The queen leaves its current location with a constant probability, i.e. the decision to move on is independent of temperature and the presence of adult workers or brood. With a certain probability (identical to that of worker bees) she will then follow a temperature gradient and move to the warmest of her neighbouring cells, but only, if that cell does not contain brood. If it does contain brood, or if the queen does not follow the temperature gradient after she decided to move, she will randomly choose one of her eight neighbour cells as her new location. This mechanism increases the probability that the queen will locate herself close to the edge of the brood nest, where on the one hand, temperatures are high enough to be suitable for brood but on the other hand, empty cells in which eggs can be laid are still available.

Thermoregulation and heat flow

Temperature changes in the model are either caused by changes in the ambient temperature, thermoregulation of worker bees or activation of the heating pads. Temperature differences cause heat flows from warmer to cooler cells. The model only considers heating activities of the bees but no cooling and hence ambient temperatures are limited to no more than 35 °C, which equals the optimal brood nest temperature.

To engage in thermoregulation, bees have to be "sitting" on a cell and not moving. If a bee sits on an empty cell, it is considered as "resting" and will maintain a body temperature of 30 °C. If it is sitting on a brood cell, it will raise its body temperature to 35 °C.

The temperature increase of a heated cell is calculated from the temperature difference between the cell and the bee sitting on it, taking a heat transfer coefficient into account. If the cell temperature is higher than the temperature of the bee, both temperatures remain unchanged. This may happen if a bee sits on an empty cell close to the brood nest.

Egg laying

Only the queen can lay eggs in the model. She will do so, if the cell she is currently on is empty and has a suitable temperature. Suitable means that its temperature is equal or above the queen's threshold temperature for egg laying. This threshold temperature is initially set to its minimal value of 29.5 °C, i.e. just below the body temperature of resting bees. Whenever the queen lays an egg, her threshold value is increased, while it drops (by a rate of 0.5 per day) when she does not lay eggs. The queen's egg laying threshold cannot exceed 34 °C.

Brood development and mortality

Every time step, the brood ages according to the time that has passed (default: 5s). As soon as a threshold age is reached, an individual will develop into the next brood stage, i.e. an egg will develop into a larva at the age of 3d, a larva will pupate at the age of 9d and the adult worker will emerge after a total of 21d of development. Immediately afterwards, the cell will be empty again and can potentially be used by the queen to lay an egg in without any further delay. As described above, the newly emerged bees do not change the number of adult workers in the simulation, i.e. they are just recorded and then disappear.

As the model focuses on brood nest patterns and does not take foraging or food stores into account, larvae are not fed. Hence, the three developmental stages do not differ in their behaviour nor trigger different behaviours in the adult bees. As a consequence, there is also no brood mortality as a result of starvation. However, brood mortality may arise, if developing individuals are not sufficiently incubated. If the mean cell temperature of a developing individual drops below a freezing threshold (30 °C) over a period of 24 hours, this individual dies and the cell is empty again.

2.3. Results

2.3.1 Brood nest formation

Shortly after the initiation of a simulation run, the bees start to accumulate, creating a positive feedback: a somewhat warmer area attracts more bees which themselves contribute to heat up this area. This also attracts the queen, who will eventually lay eggs. The presence of brood results in further heating activity of workers and hence more cells will reach a temperature suitable for egg laying. As a consequence of these processes, a closed brood nest is formed, as it can be observed in real colonies. Fig. 2.5 compares the development of the brood nest on a simulated and a real comb over 24 days (from first egg laying to emergence of adult workers and the beginning of a new brood cycle).

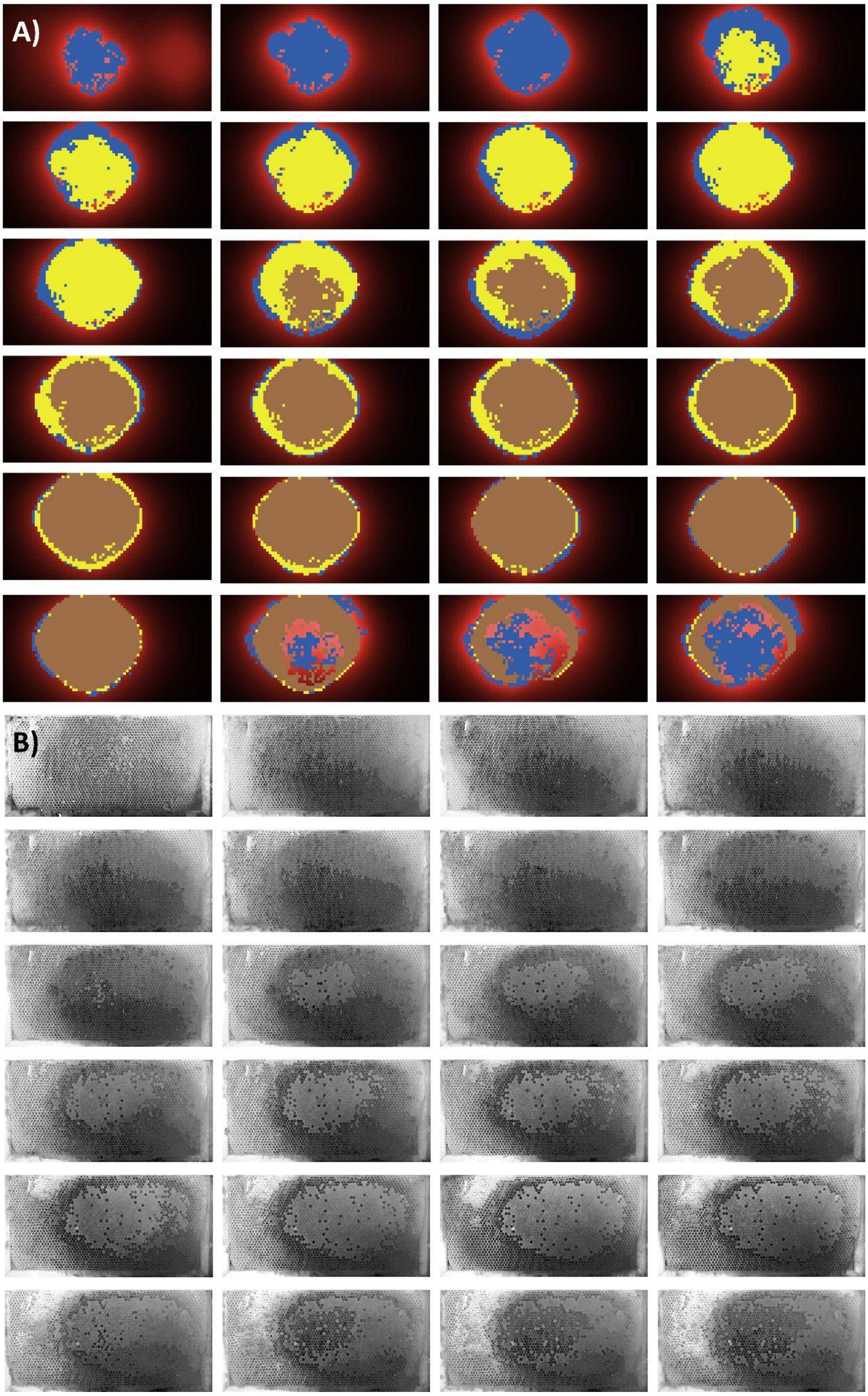

Fig. 2.5: A) Example of the development of the brood nest over 24 days under default conditions with 1500 workers being present. Eggs are shown in blue, larvae in yellow and pupae in brown. On day 22, a large proportion of the pupae have emerged as adults and the empty space is used for egg laying. **B)** Photos of the brood nest development over 24 days from one of our observation hives (31.08. - 23.09.2021). Please note that only capped brood (pupae) is clearly visible in these photos. Both, capping of the first brood cells and dissolving of the centre of the brood nest match the simulation well.

2.3.2 Impact of worker numbers and ambient temperature on brood nest size

We tested the impact of the number of worker bees (50 - 2000) and ambient temperature (20 °C and 25 °C) on the size of the brood nest under otherwise default conditions (Fig 2.6). Simulations ran for 10 days (N = 3). The results suggest that there is a minimal work force required in order to successfully raise brood. The minimal number of worker bees depends on the ambient temperature. At an ambient temperature of 20 °C, there need to be more than 50 bees available for thermoregulation, otherwise, no eggs will be laid.

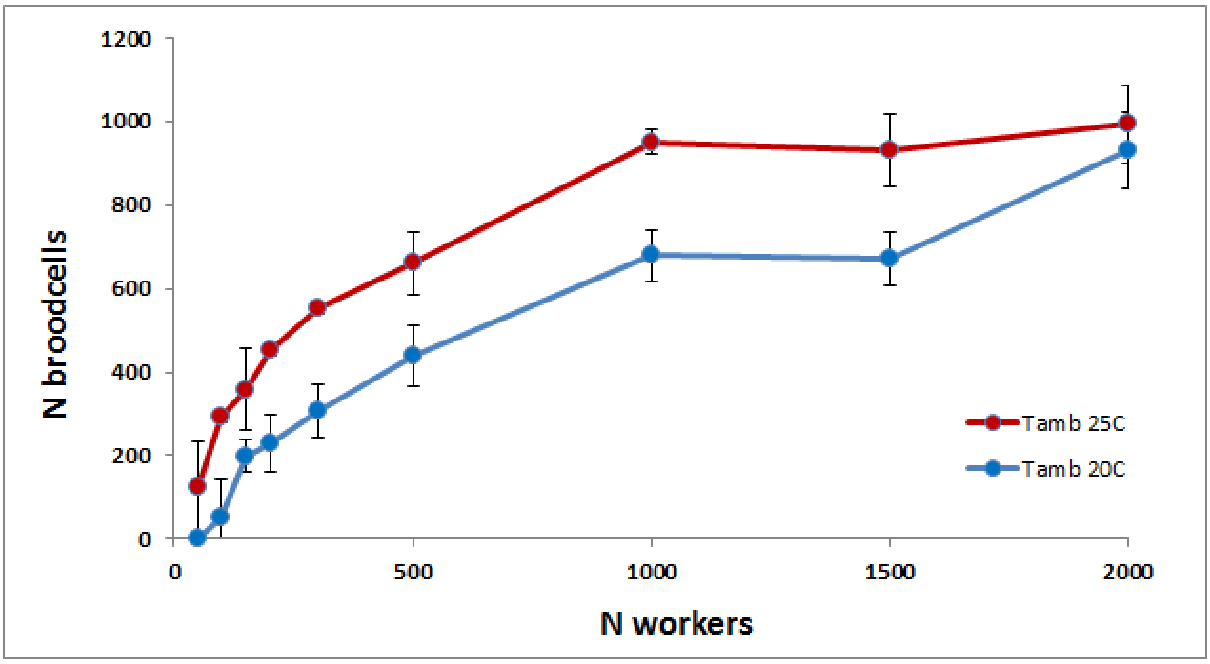

Fig. 2.6: Impact of number of workers and ambient temperature on the brood nest size after 10 days (N = 3). No brood at all is produced with 50 workers at 20 °C.

2.3.3 Heating a defined brood nest

We compared the model output to experimental data on thermoregulation of brood. We used a data set from Becher et al. (2010), where a defined piece of capped brood was inserted in an empty cell and a certain number of bees (here: 150 in-hive bees) were added to the comb at ambient temperatures of ca. 25 °C. Temperatures were then measured for about 20 hours on the back side of the comb with a temperature device described in Becher & Moritz (2009). We mimicked this setup in our HIVEOPOLIS Brood Nest Model by removing the queen and adding a rectangular area with brood. Size and dimension as well as the number of temperature sensors were adjusted according to the experimental design, the number of bees was set to 150 and the model ran for 20 simulated hours. The results show that the preference of bees heating the brood was captured well by the model (Fig. 2.7). This is particularly interesting, as the model does not consider brood pheromone, i.e. - in contrast to real bees - the model bees are not attracted to the brood as such. However, if model bees heat a brood cell, they try to raise the temperature to 35 °C (instead of 30 °C of empty cells). As they have a tendency to walk uphill in a temperature gradient, they finally accumulate over the brood nest.

The comparison of simulated and empirical data also reveals that this accumulation of bees over the brood might be more pronounced in the model, where higher brood temperatures are reached, while the area outside of the brood nest remains colder. However, experimental data might be approximately 1.4 °C lower on the back side of the comb, where the sensors were placed and no bees had access to, than on the front side (Becher & Moritz 2009).

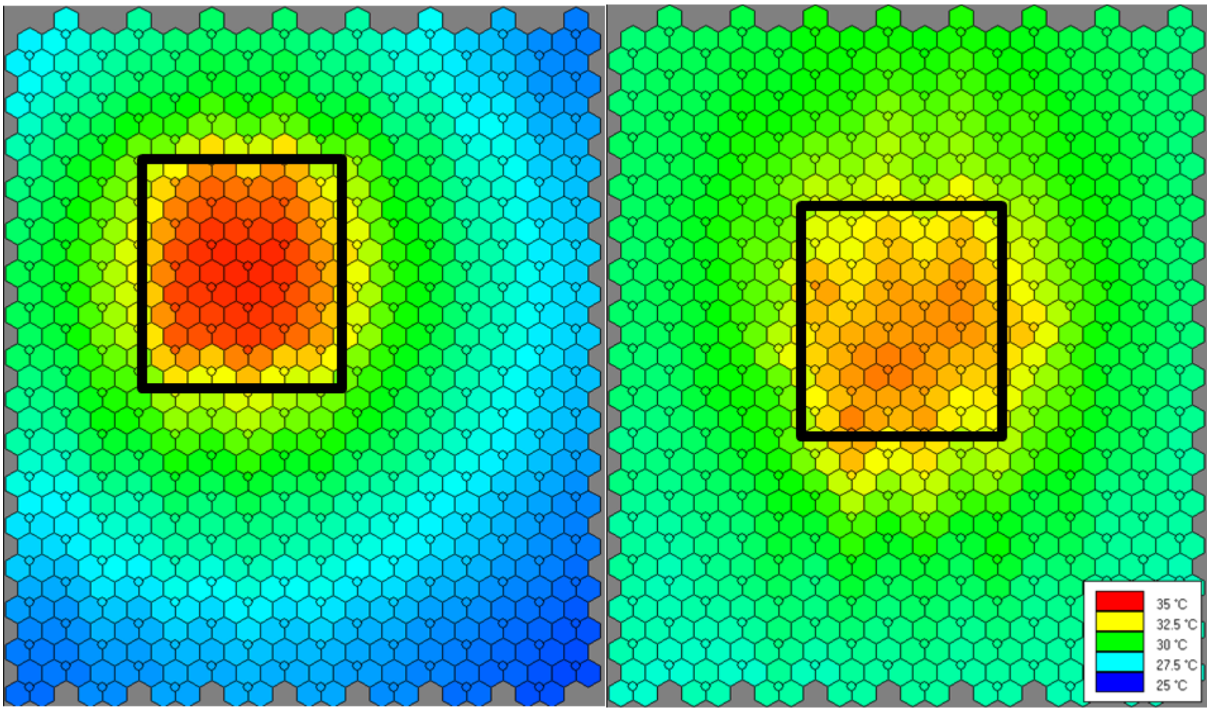

Fig. 2.7: Comparison of simulated (left) and experimental (right) brood nest temperature data. The experimental setup by Becher et al. (2010) consisted of a defined piece of capped brood (indicated by the black frame) that was placed in an otherwise empty comb and 150 (in-hive) bees were added. Temperature measurements with 256 sensors took place on the back side of the comb, where bees had no access to, which resulted in ca. 1.4 °C lower temperatures than on the front side (Becher & Moritz 2009). We then mimicked this experimental setup with our Brood Nest Model. The graphs were created using a software tool by Becher & Moritz (2009) and show the temperature distributions after ca. 20 hours.

3. Estimation of brood numbers

3.1 Objectives of the Brood-Estimator Tool

The Brood-Estimator Tool is a relatively simple model that allows us to draw a number of conclusions on various aspects of the brood nest, solely based on the temperature recordings of the thermal sensors of our Sensor/Actuator combs.

We try to achieve the following goals with this tool:

- determine to size of the brood nest
- identify egg laying events
- identify brood mortality
- keep track of existing brood
- combine these data to estimate amount, age and developmental stage of brood on the various sections of a sensor/actuator comb
- inform the colony module of the HO Core Model to update the brood nest information and number of newly emerged adult bees
- identify potential threats to the colony due to brood mortality and inform the user

3.2 Sensor/Actuator combs

A second generation brood nest module prototype comb was used for collecting the data for the brood estimation described hereafter. Among other sensors, 64 temperature sensors (55 equally-spaced ones and another nine that are tightly packed in the so-called 'high-density patch') are evenly distributed over the surface of these combs (see also D5.1 chapter 3.1.2 "Selecting the density of temperature sensors" and Fig. 3.1). The sensors sample the temperature readings in a 10-sec interval. In addition to the temperature sensors, the combs are also equipped with 10 heating actuators (for more details see also D5.1 chapter 3.3).

Ultimately the Sensor/Actuator combs will be integrated into a HIVEOPOLIS hive. In the current project phase, the Sensor/Actuator combs are still in use in observation hives so that the behavior of the animals can be compared with the temperature data via camera recordings as ground proof. Additionally the influence of the artificially supplied heat actuation on the bee behavior can be quantified this way. More information on the sensor/actuator honeycombs used to collect temperature data "inside" the bee colony can be found in Deliverable D5.1 "Design of the brood nest module", which describes the design of the brood nest module in more detail.

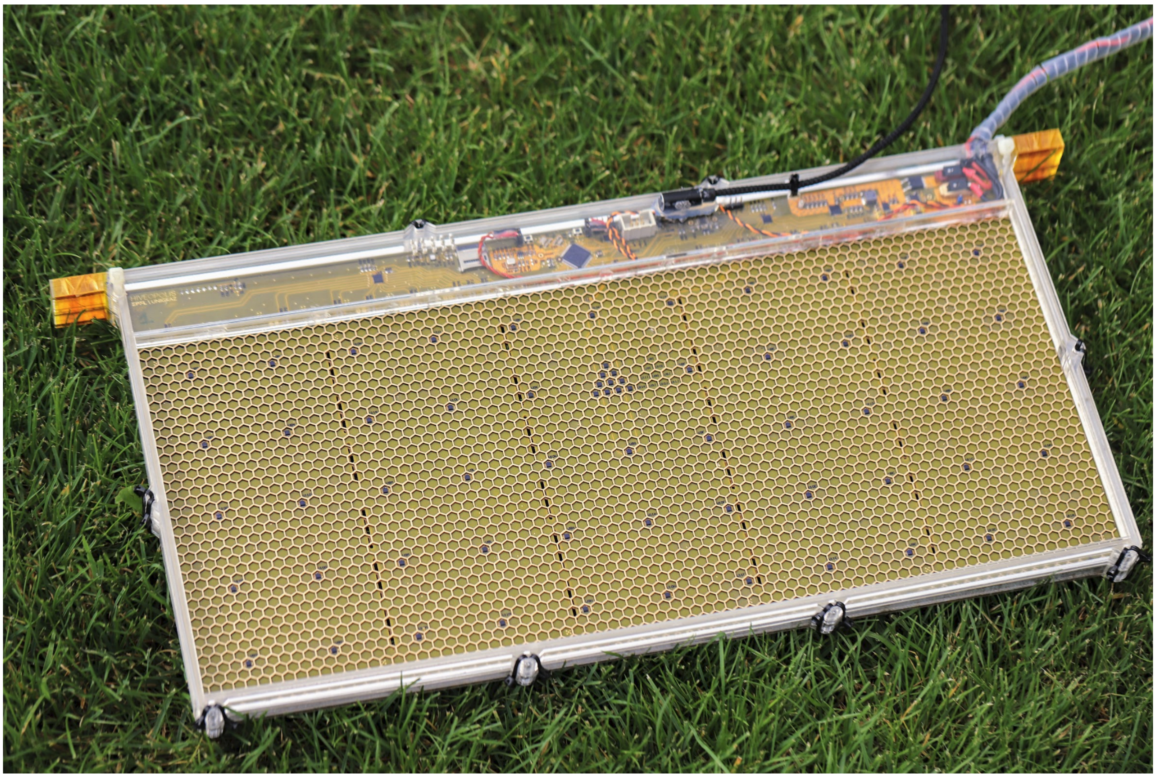

Fig. 3.1: Second prototype of the Sensor/Actuator combs that collected temperature data used to estimate the brood. Depicted outside of a hive and before bees constructed wax cells on it.

3.3 Description of the Brood-Estimator Tool

The Brood-Estimator Tool assesses the amount of brood and related data from brood comb temperature recordings. The temperature input can either come from the virtual sensors of the Brood Nest Model (Chapter 2) created during a simulation run, or it can be based on experimental data, loaded into the model. We first describe the processes when temperature data is the product of a simulation run and then how experimental data can be imported.

3.3.1 Brood estimations

Each virtual sensor in the Brood Nest Model is surrounded by a rectangular area of cells, associated with that sensor. The sensor is approximately in the center of this area and the dimensions of the area depends on the dimensions of the comb and the number and positioning of the sensors. The areas are of identical size for all sensors and as big as possible without overlapping with the areas of the neighbouring sensors.

Unspecific estimation of the brood

Whenever the virtual sensor in the Brood Nest Model records the temperature (defined by a recording frequency usually set to 10 minutes), the number of brood cells in each sensor area is estimated. It is assumed that the proportion of cells containing brood in a sensor area increases linearly from 0 at the "resting" temperature of the bees (30 °C) to 1 at the ideal brood nest temperature (35 °C). Multiplying this proportion with the number of cells in the sensor area results in the amount of brood around a sensor and summing these numbers up over all virtual sensors results in an estimate of the total brood nest size. As this is solely based on the simulation of the Brood Nest Model, we can compare the "actual" (i.e. simulated) number of brood cells with the number of brood cells we estimate from the sensor temperatures. While this method allows us to estimate the total amount of brood present in the colony, it gives no information on its age distribution, developmental stages of mortality. Deriving these factors from the temperature data will be described in the next section.

Estimation of brood cohorts and brood mortality

In order to learn more about the age distribution or developmental stages of the brood, we first have to identify egg laying events and then keep track of the developing brood.

At the beginning of a new simulation day, changes in the number of estimated brood cells over the past 24 hours within the area of each virtual temperature sensor are recorded. If the number of brood cells has increased, the difference is interpreted as the number of newly laid eggs. This number is then - separately for each virtual sensor - saved as the first entry of a list. Hence, the number of entries in that list increases by 1 every day until the maximal length of 21 entries is reached, reflecting the 21 days of brood development. From day 22 onwards, the last entry is interpreted as the number of newly emerged adult workers and then deleted from the list. To determine the number of developmental stages in each sensor area, we assume that cohorts 1 to 3 are eggs, 4 to 9 are larvae and 10 to 21 are pupae. By summing up the brood numbers of each sensor, we can determine the egg laying rate and the total number of eggs, larvae and pupae present.

If the number of estimated brood shrinks from one day to the next, we assume that the difference is due to brood mortality and the proportion of supposedly dead brood is calculated. As it is unknown which age cohorts may have been subject to brood mortality, it is applied to all cohorts, i.e. the all entries of the list, keeping track of the brood cohorts in the area of a given sensor are multiplied by the estimated proportion of dead brood.

3.3.2 Data import from experimental colony

Temperature data from the experimental hives is imported via a CSV-file. Two file formats are currently supported:

File format EPFL: The file contains a header, one column with the date and time (dd/mm/yyyy mm:ss), and 64 columns of temperature data from a Sensor Actuator Frame with 64 temperature sensors.

File format UNIGRAZ: The file contains a header, one column with the date (dd/mm/yyyy), one column with the time (mm:ss), and six columns of temperature data from a Sensor/Actuator Comb with six temperature sensors.

Irrespective of the file format, the time difference between each data set (i.e. between each row) is automatically determined after the file has been loaded, but it needs to be in the range of >= 1 minute and <= 59 minutes.

These sensor temperatures are then treated in the same way as those sensor temperatures, which are derived from a simulation run of the Brood Nest Model to assess the amount and age distribution of the brood (section 3.3.1).

3.3.3 Data export

Estimates of daily cohort sizes of the brood are written in a text file to be accessible by the central colony model. The text file contains one data line for each day and a header with three columns: 1) the time step (day, starting on 1st January of the first year as 1)), 2) a list with 21 entries defining the number of bees in each age class of the brood and 3) the number of newly emerged workers.

3.4 Application

3.4.1 Comparison of estimated and simulated brood numbers

We tested whether it would be possible to estimate the number of eggs, larvae and pupae based on the temperature distribution on a brood comb by comparing the results of the Brood Estimator Tool with the simulated results of the Brood Nest Model. We ran the Brood Nest Model for 100 days under default conditions with 1500 worker bees present and at a constant ambient temperature of 25 °C.

We used the recordings of the virtual temperature sensors of this simulation run as input for the Brood Estimator Tool, to assess the daily egg laying, brood mortality and number of new workers hatched, as well as how many eggs, larvae and pupae were present. At the same time, we determined the actual numbers of those state variables in the simulation. Figures 3.2 to 3.7 compare the simulated numbers (i.e. directly from the Brood Nest Model) with the estimated numbers (i.e. derived from the Brood Nest Estimator, based on the simulated temperatures).

Overall, we get a good match of simulated and estimated brood numbers. This means that the method works - at least for simulated data from the Brood Nest Model - well to identify egg laying events and subsequently estimate the number of eggs, larvae, pupae and new adults as well as the brood mortality.

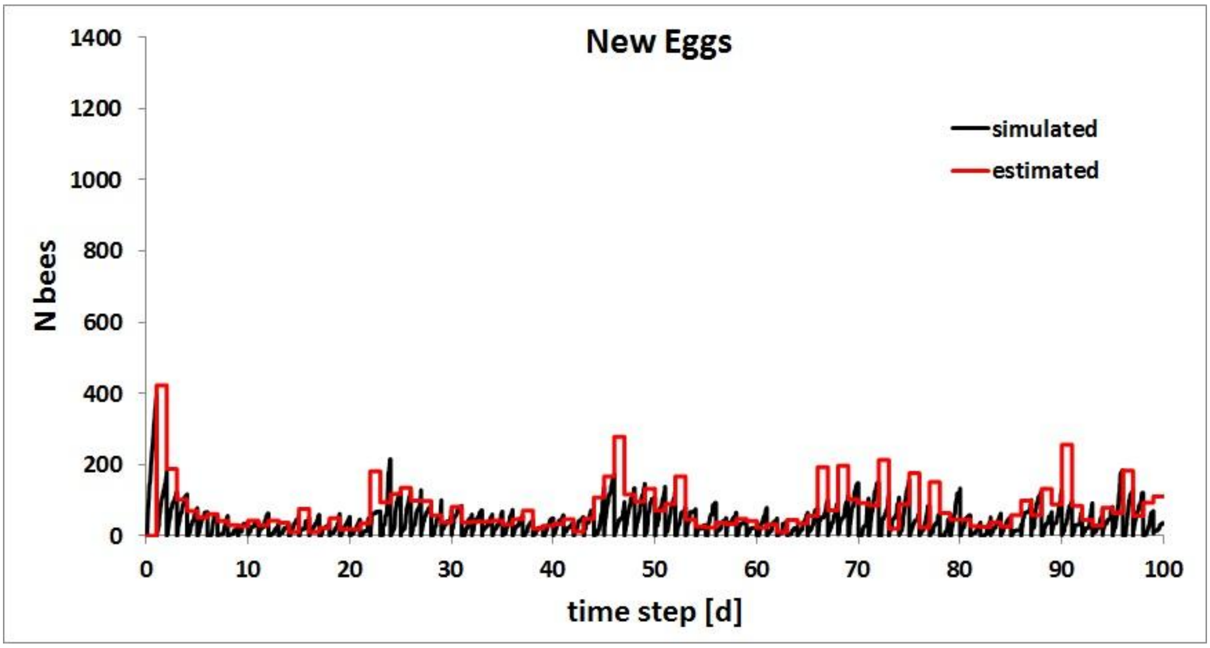

Fig. 3.2: Comparison of the simulated daily egg laying in the Brood Nest Model with the estimated egg laying, using the Brood Estimator Tool, which takes the virtual brood nest temperatures as input. Please note that numbers of the Brood Estimator Tool are only updated once a day, while the actual numbers in the simulation are recorded every 10 minutes.

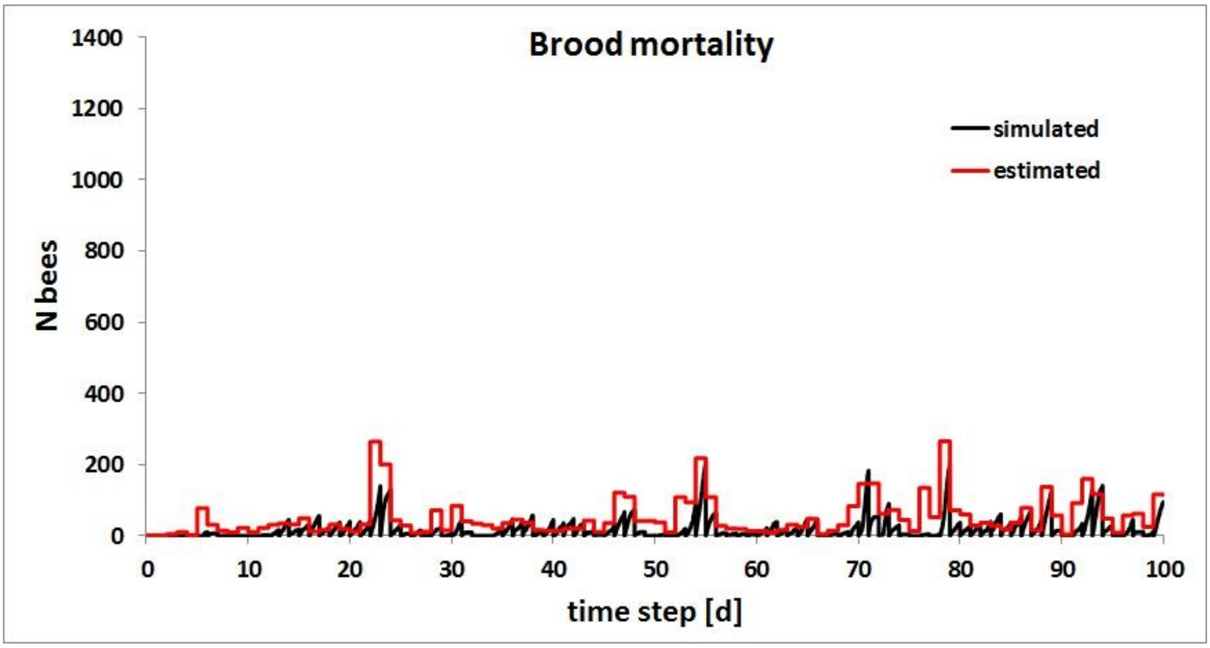

Fig. 3.3: Comparison of the simulated brood mortality in the Brood Nest Model with the estimated brood mortality, using the Brood Estimator Tool, which takes the virtual brood nest temperatures as input.

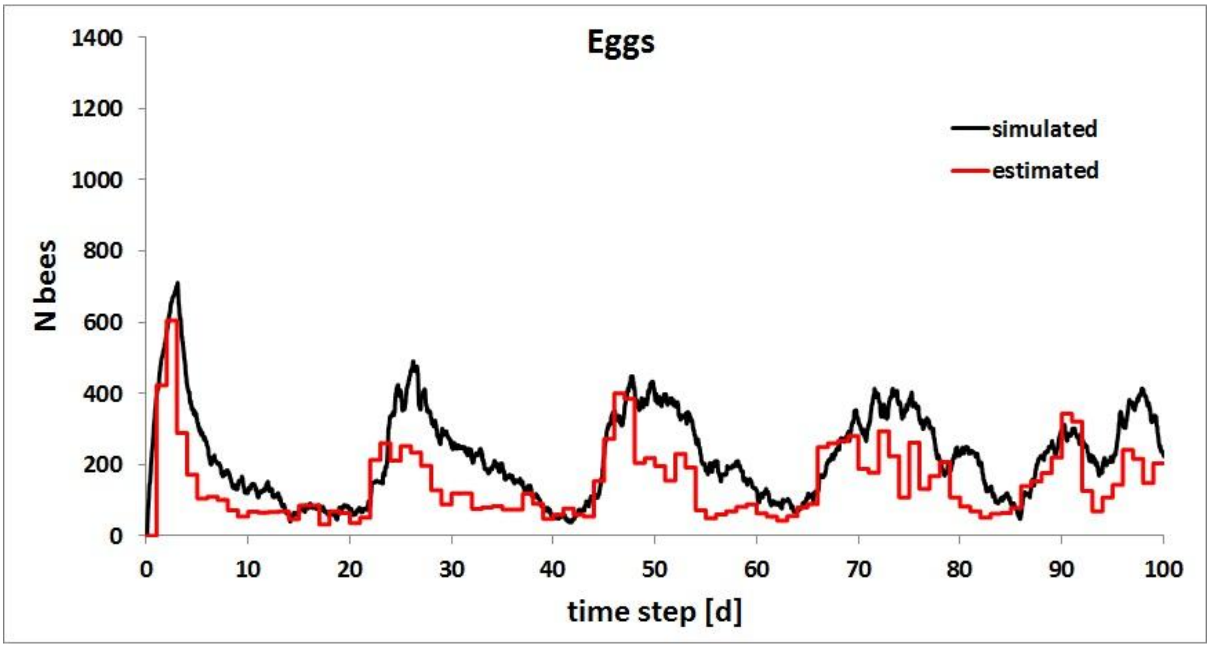

Fig. 3.4: Comparison of the simulated number of eggs in the Brood Nest Model with the estimated number of eggs, using the Brood Estimator Tool, which takes the virtual brood nest temperatures as input.

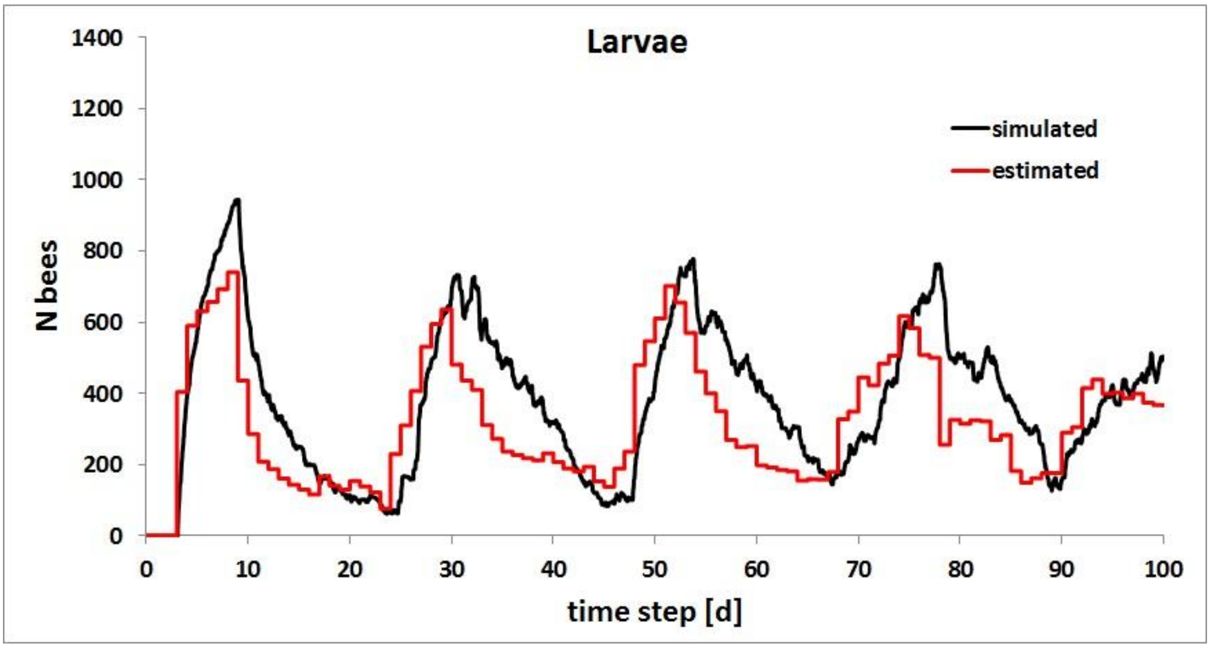

Fig. 3.5: Comparison of the simulated number of larvae in the Brood Nest Model with the estimated number of larvae, using the Brood Estimator Tool, which takes the virtual brood nest temperatures as input.

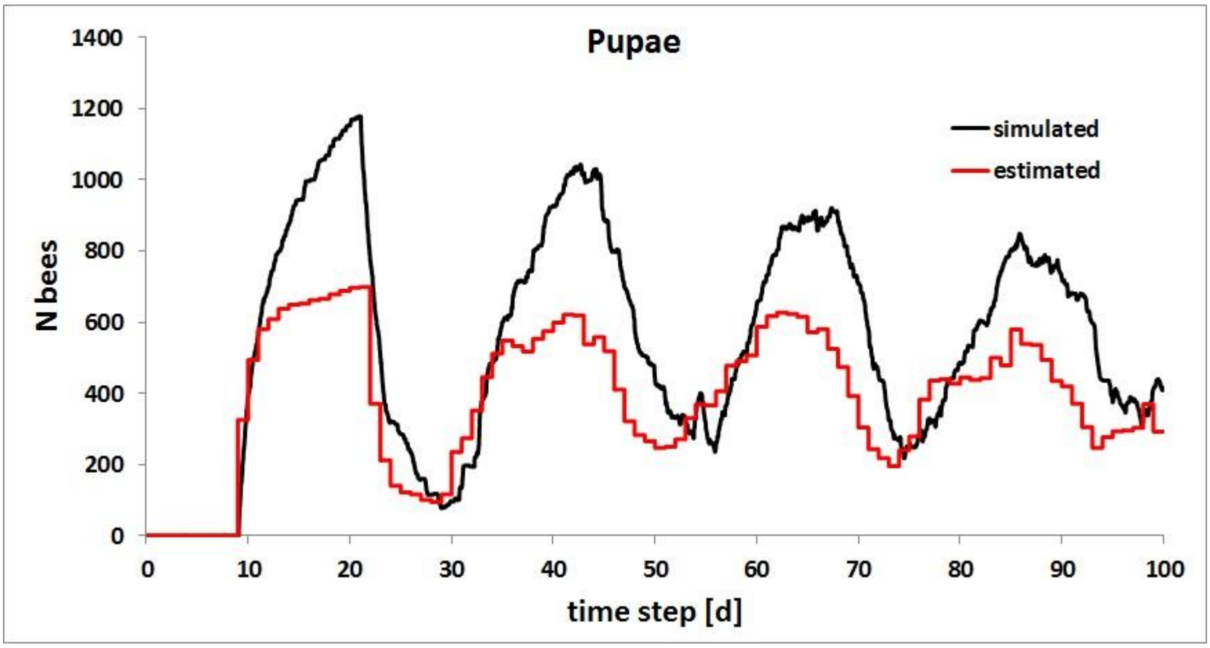

Fig. 3.6: Comparison of the simulated number of pupae in the Brood Nest Model with the estimated number of pupae, using the Brood Estimator Tool, which takes the virtual brood nest temperatures as input.

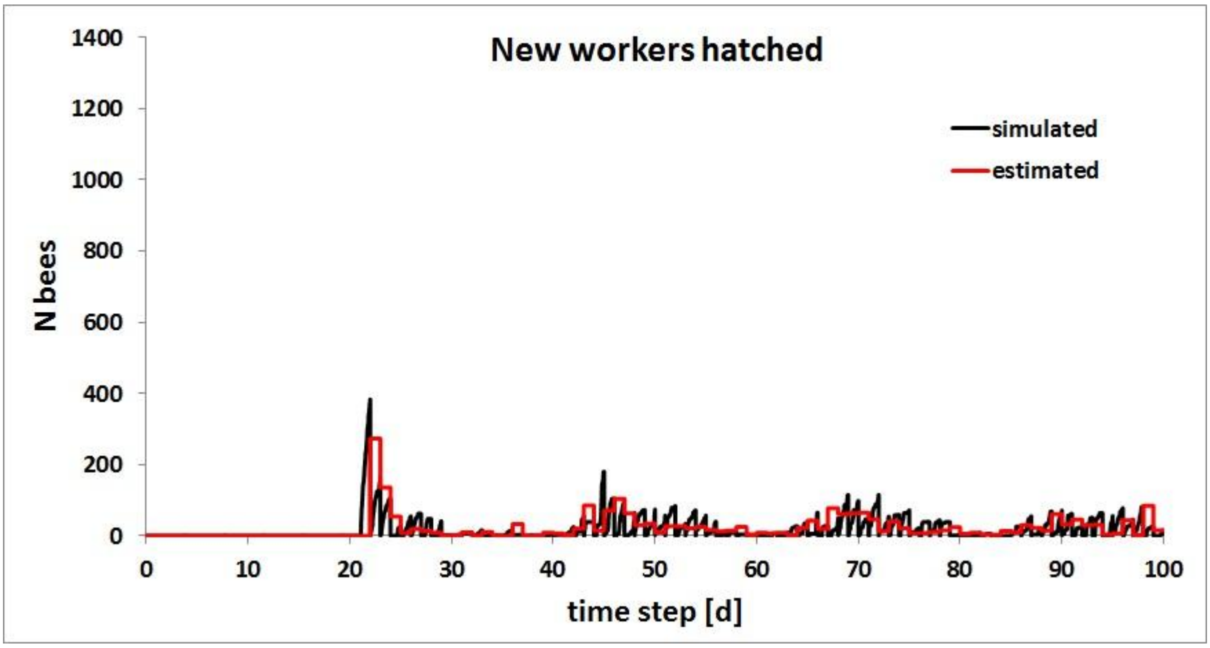

Fig. 3.7: Comparison of the simulated number of newly hatched workers in the Brood Nest Model with the estimated number of newly hatched workers, using the Brood Estimator Tool, which takes the virtual brood nest temperatures as input.

3.4.2 Comparison of estimated and real brood numbers

While the Brood Nest Estimator tool provides reasonable brood estimates in a simulated environment, it is not clear yet if it is also useful in an experimental setup. We hence used one month (September 2020) of temperature recordings from our EPFL sensor/actuator comb and automatically taken photos from this comb to test the quality of these estimations. While the resolution of those photos does not allow to identify eggs or larvae, capped brood cells are clearly visible (Fig. 3.8).

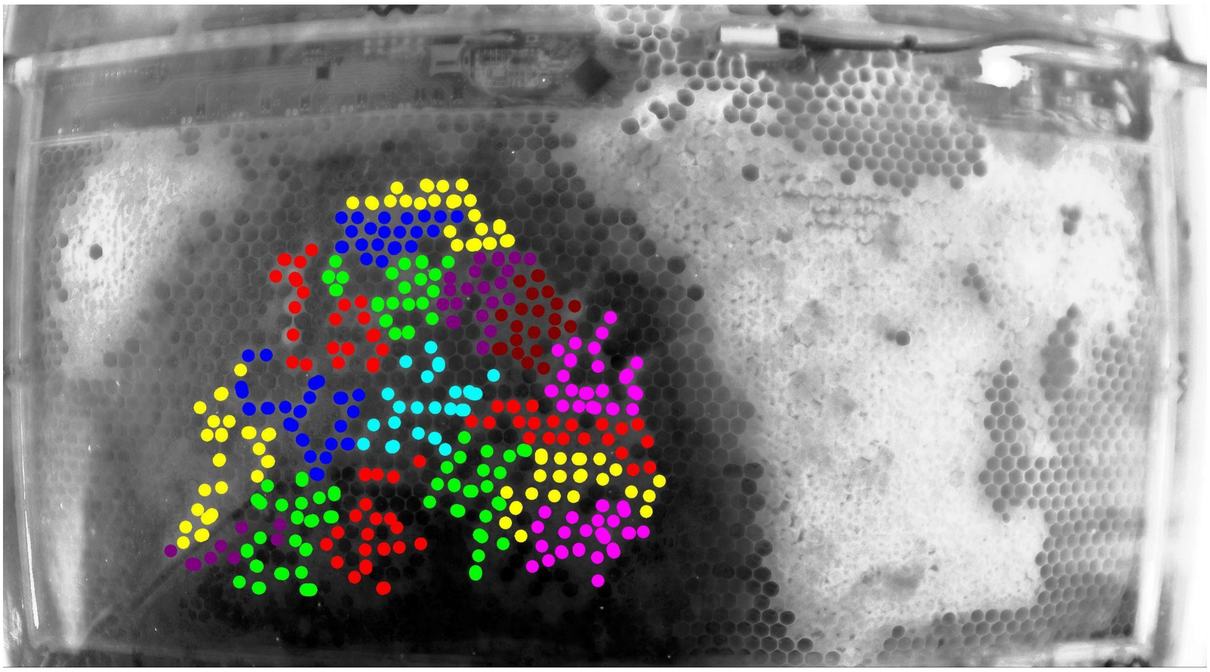

Fig. 3.8: Example of an automatically taken photo of a sensor/actuator comb, with a brood nest being present (26.09.2020). 328 capped brood cells containing pupae have been visually identified and manually marked, using a photo editing software.

We were then able to compare the estimated number of pupae with the actual number of capped brood cells (Fig. 3.9). We find a good match of estimated and actual number of capped brood, which shows that the temperature distribution on the brood comb can be used to get reasonably accurate information on the brood nest size, the developmental stages of the brood and the number of new workers hatching on a daily basis.

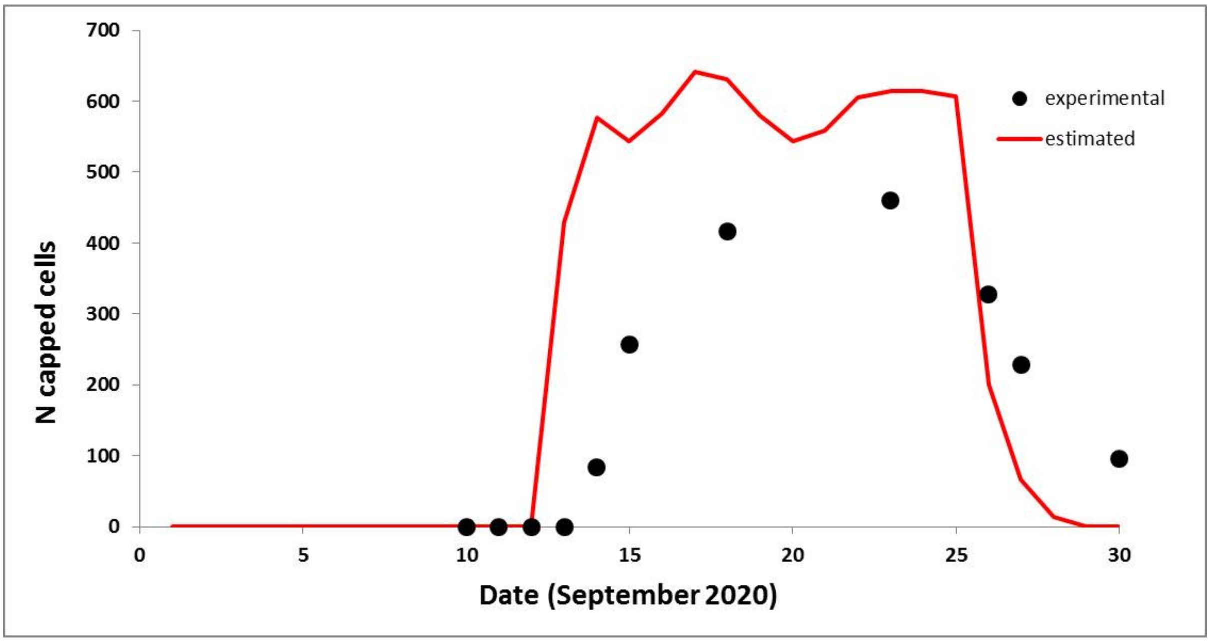

Fig. 3.9: Comparison of estimated and actual number of capped (pupal) cells on a sensor/actuator comb. The estimates were calculated from the temperature distribution on the sensor/actuator comb during September 2020, using the Brood Estimator Tool. Experimental data were derived from automatically taken photos of one side of that comb. The brood nest was approximately symmetrical on both sides of the comb. This shows that - only using the temperature distribution on the comb - it is possible to approximately assess not only the size of a brood nest but also the age distribution and developmental stages of the brood.

4. Prediction of colony dynamics

In order to not reinvent the wheel, we used the BEEHAVE model (Becher et al., 2014) as a starting point for BEEHAVEOPOLIS, the central HIVEOPOLIS bee model. In BEEHAVEOPOLIS, data and model output of the various modules come together and drive the simulation of the colony dynamics.

4.1 Suitability of BEEHAVE as starting point for the HIVEOPOLIS central bee model

BEEHAVE is a mixed, cohort- and agent-based model that simulates colony dynamics and foraging behaviour of a single honeybee colony. Based on a seasonal daily egg-laying rate, it follows the development of 1-day cohorts of bees through their development from eggs via larvae and pupae to adults. It distinguishes between workers and drones and between young in-hive workers and older foragers. In-hive bees are responsible for brood care, while foragers (implemented as super-individuals, i.e. agents, representing 100 bees) explore the landscape to collect nectar and pollen from various food sources. Varroa mites and varroa transmitted viruses can also be taken into account, as well as various beekeeping options.

BEEHAVE has been evaluated by the European Food Safety Authority (EFSA, 2015) and by Agatz et al. (2019) and validated by Schmolke et al. (2020). It has been applied by researchers to simulate the impact of pesticides (e.g. Thorbek et al. 2016, Prado et al. 2019), forage availability (Horn et al., 2016, Horn et al. 2020), Asian hornets (Requier et al. 2018), antibiotic treatment (Bulson et al. 2020) and other factors. It has also been used by EFSA to model the background variability of colony sizes in 19 European countries in the context of pesticide risk assessment (EFSA 2021).

As BEEHAVE is a well-established, mechanistic model that contains more processes than any other currently available honeybee model (EFSA, 2021, Appendix A), it seems to be an ideal starting point for the HIVEOPOLIS central colony model.

4.2 Changes to BEEHAVE: link with the Brood-Estimator Tool

To integrate data from the brood nest module, the BEEHAVE model (Becher et al., 2014) had to be modified to import the input files created by the Brood-Estimator Tool (Section 3.3.3).

These files are now read in and saved during the setup process of BEEHAVE. During each day of the simulation it is checked whether empirical brood nest data are available. If this is the case, today's egg laying and the brood numbers in the model are adjusted accordingly. Each of the 21 brood cohorts in the model updates the number of bees it represents, which might be an increase or a decrease in number.

For the pupae, it needs to be distinguished whether or not they have been infected with a virus. When updating the bee numbers of pupal cohorts, it is hence assumed that the ratio of healthy to infected bees in each cohort remains unchanged.

Once bee numbers have been updated, the simulation continues and the bees develop and behave as defined by the model without further changes, until another update of bee numbers, based on the empirical input, takes place. Indirectly however, updating brood numbers can have substantial impacts, especially if the deviation is great. For example, the age of first foraging (i.e. when in-hive bees develop into foragers) may increase, if brood is added or it may decrease, if brood is removed. Also the foraging behaviour may change, as larvae have to consume enough pollen to develop into pupae, and hence adding young brood stages may increase the colony's pollen foraging efforts.

4.3 Core-model simulations with updates from the Brood-Estimator Tool

After the central honeybee model was modified to integrate experimental data from the brood nest module, we then tested it by importing the estimated brood numbers from October 2020 (Section 3.4). As no data on resource availability for the experimental hive was available, we compared runs under the default setting of the model with or without modifying brood numbers in October (Fig. 4.1). Under default settings, two food sources are provided, one in 1500m distance from the hive, starting to blossom earlier in the season and a second one in 500m distance flowering later. Weather (foraging) conditions are based on empirical data from 2009 at Rothamsted Research, Harpenden, UK.

Without updating the brood numbers in the simulation run, the already small brood nest smoothly shrinks during autumn and winter. In the real colony, however, no brood was present at all on 1st October when the experimental data set starts. A short period of intense egg laying did set in a few days later, though, resulting in a high peak in the brood nest size. From November onwards, the simulation is no longer updated with empirical data and hence the amount of brood drops quickly. Consequently, the number of adult bees in the run that includes real brood nest data, is first lower than under default setting, but then increases sharply during November, resulting in a larger colony at the end of the year.

This result shows that we are not only able to estimate the brood nest size and age distribution from the temperature gradients recorded with our Sensor/Actuator combs, but that we can also feed this information into the HIVEOPOLIS core model to predict colony development and performance. In future, brood nest data will be updated on a daily basis throughout the year and further information regarding e.g. weather conditions and forage availability will also be taken into account.

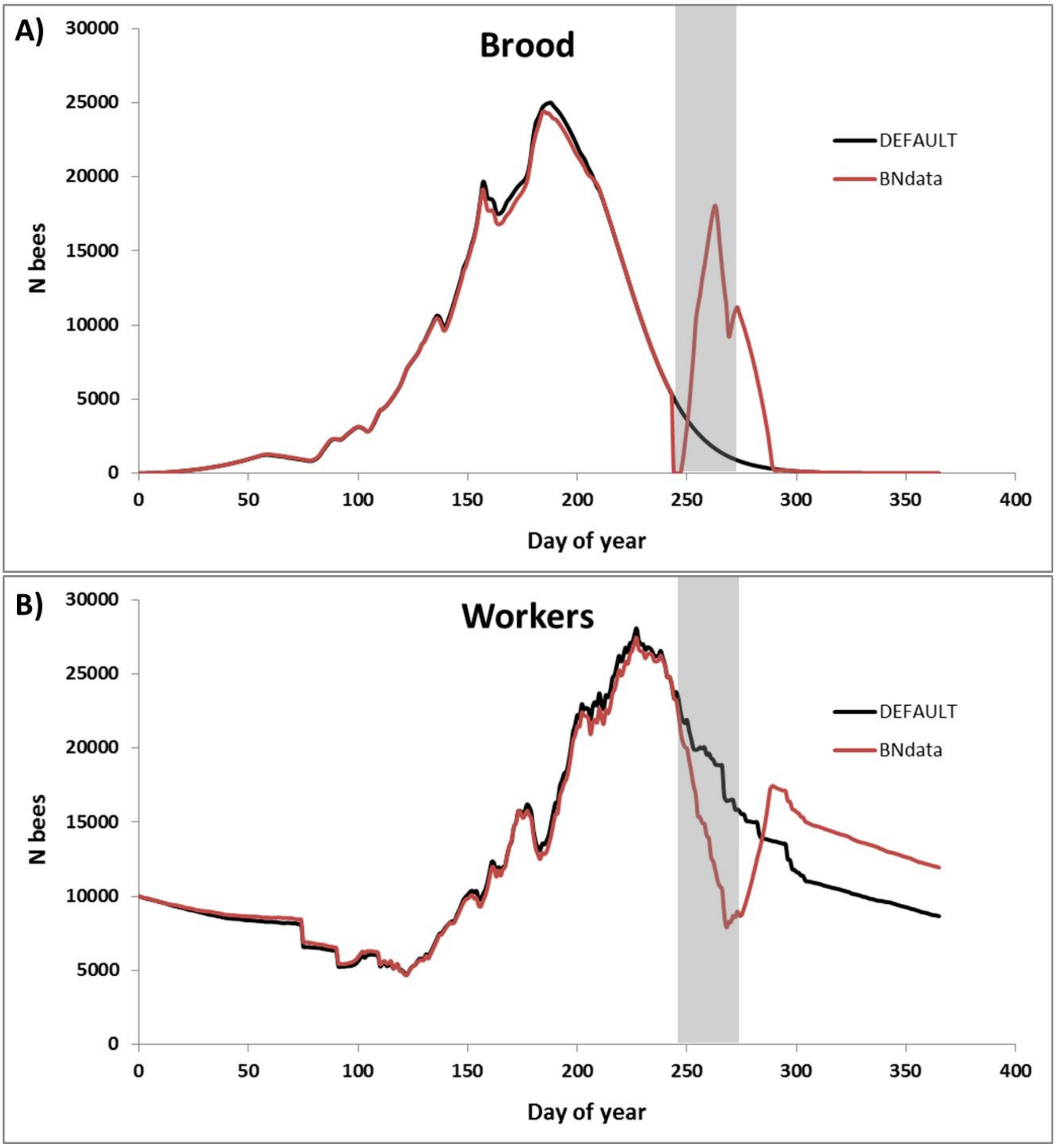

Fig. 4.1: Comparison of colony dynamics simulations over one year with (red) or without (black) importing experimental brood numbers into the model (N = 20). A) shows the amount of brood (eggs, larvae, pupae), B) the number of workers (in-hive bees and foragers) under the default BEEHAVE setup. The shaded area marks the time when experimental brood nest data is imported on a daily basis.

Bibliography

Agatz, A., Kuhl, R., Miles, M., Schad, T., & Preuss, T. G. (2019). An evaluation of the BEEHAVE model using honey bee field study data: Insights and recommendations. Environmental Toxicology and Chemistry, 38(11), 2535–2545. https://doi.org/10.1002/etc.4547

Becher, M.A. and Moritz, R.F., (2009). A new device for continuous temperature measurement in brood cells of honeybees (*Apis mellifera*). Apidologie, 40(5), 577-584.

Becher, M. A., Hildenbrandt, H., Hemelrijk, C. K., & Moritz, R. F. (2010). Brood temperature, task division and colony survival in honeybees: A model. Ecological Modelling, 221(5), 769-776.

Bulson, L., Becher, M. A., McKinley, T. J., & Wilfert, L. (2021). Long‐term effects of antibiotic treatments on honeybee colony fitness: A modelling approach. Journal of Applied Ecology, 58(1), 70-79.

EFSA Panel on Plant Protection Products and their Residues (PPR). (2015). Statement on the suitability of the BEEHAVE model for its potential use in a regulatory context and for the risk assessment of multiple stressors in honeybees at the landscape level. EFSA Journal, 13(6), 4125

EFSA (European Food Safety Authority), Ippolito, A., Focks, A., Rundlöf, M., Arce, A., Marchesi, M., Neri, F.M., Szentes, C., Rortais, A. and Auteri, D. (2021). Analysis of background variability of honeybee colony size. EFSA supporting publication 2021:EN-6518. 79pp. doi:10.2903/sp.efsa.2021.EN-6518

Ferrari, S., Silva, M., Guarino, M., & Berckmans, D. (2008). Monitoring of swarming sounds in bee hives for early detection of the swarming period. Computers and electronics in agriculture, 64(1), 72-77.

Gil-Lebrero, S., Quiles-Latorre, F. J., Ortiz-López, M., Sánchez-Ruiz, V., Gámiz-López, V., & Luna-Rodríguez, J. J. (2017). Honey bee colonies remote monitoring system. Sensors, 17(1), 55.

Hambleton JI (1925) The effect of weather upon the change in weight of a colony of bees during the honey flow, United States Department of Agriculture, Dept. Bull. No. 1339.

Horn, J., Becher, M. A., Kennedy, P. J., Osborne, J. L., & Grimm, V. (2016). Multiple stressors: using the honeybee model BEEHAVE to explore how spatial and temporal forage stress affects colony resilience. Oikos, 125(7), 1001-1016.

Horn, J., Becher, M. A., Johst, K., Kennedy, P. J., Osborne, J. L., Radchuk, V., & Grimm, V. (2021). Honey bee colony performance affected by crop diversity and farmland structure: a modeling framework. Ecological Applications, 31(1), e02216.

Jarimi, H., Tapia-Brito, E., & Riffat, S. (2020). A Review on Thermoregulation Techniques in Honey Bees'(Apis Mellifera) Beehive Microclimate and Its Similarities to the Heating and Cooling Management in Buildings. Future Cities and Environment, 6(1).

Kridi, D. S., Carvalho, C. G. N. D., & Gomes, D. G. (2014). A predictive algorithm for mitigate swarming bees through proactive monitoring via wireless sensor networks. In Proceedings of the 11th ACM symposium on Performance evaluation of wireless ad hoc, sensor, & ubiquitous networks (pp. 41-47).

Kviesis, A., Komasilovs, V., Komasilova, O., & Zacepins, A. (2020). Application of fuzzy logic for honey bee colony state detection based on temperature data. Biosystems Engineering, 193, 90-100.

Meikle, W. G., & Holst, N. (2015). Application of continuous monitoring of honeybee colonies. Apidologie, 46(1), 10-22,.

Meikle, W. G., Holst, N., Colin, T., Weiss, M., Carroll M. J., et al. (2018) Using within-day hive weight changes to measure environmental effects on honey bee colonies. PLOS ONE 13(5): e0197589.

Prado, A., Pioz, M., Vidau, C., Requier, F., Jury, M., Crauser, D., Brunet, J.-L., Le Conte, Y., & Alaux, C. (2019). Exposure to pollen-bound pesticide mixtures induces longer-lived but less efficient honey bees. Science of the Total Environment, 650, 1250–1260. https://doi.org/10.1016/j.scito tenv.2018.09.102

Requier, F., Rome, Q., Villemant, C., & Henry, M. (2020). A biodiversity-friendly method to mitigate the invasive Asian hornet's impact on European honey bees. Journal of Pest Science, 93(1), 1-9.

Schmolke, A., Abi-Akar, F., Roy, C., Galic, N., & Hinarejos, S. (2020). Simulating honey bee large-scale colony feeding studies using the BEEHAVE model—Part I: Model validation. Environmental toxicology and chemistry, 39(11), 2269-2285.

Seeley, T. D. and Heinrich, B. (1981). Regulation of temperature in the nests of social insects. In: Insect Thermoregulation (ed. Heinrich, B.), pp. 159–234. NewYork: Wiley

Seeley, T. D., Kleinhenz, M., Bujok, B., & Tautz, J. (2003). Thorough warm-up before take-off in honey bee swarms. Naturwissenschaften, 90(6), 256-260.

Seeley, T.D. and Visscher, P.K. (1985), Survival of honeybees in cold climates: the critical timing of colony growth and reproduction. Ecological Entomology, 10: 81-88.

Stabentheiner, A., Kovac, H., & Brodschneider, R. (2010). Honeybee colony thermoregulation–regulatory mechanisms and contribution of individuals in dependence on age, location and thermal stress. PLoS one, 5(1), e8967.

Stalidzans, E. and Berzonis, A. (2013). Temperature changes above the upper hive body reveal the annual development periods of honey bee colonies. Computers and electronics in agriculture, 90, pp.1-6.

Tautz, J., Maier, S., Groh, C., Rössler, W., & Brockmann, A. (2003). Behavioral performance in adult honey bees is influenced by the temperature experienced during their pupal development. Proceedings of the National Academy of Sciences, 100(12), 7343-7347.

Thorbek, P., Campbell, P. J., & Thompson, H. M. (2017). Colony impact of pesticide‐induced sublethal effects on honeybee workers: A simulation study using BEEHAVE. Environmental toxicology and chemistry, 36(3), 831-840.

Wilensky, U. (1999). Netlogo. Center for Connected Learning and Computer-based Modeling Northwestern University.

Zacepins, A., Brusbardis, V., Meitalovs, J., & Stalidzans, E. (2015). Challenges in the development of Precision Beekeeping. Biosystems Engineering, 130, 60-71.