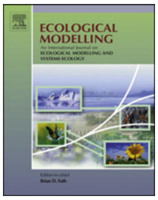
Ecological Modelling 221 (2010) 769–776

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel



Brood temperature, task division and colony survival in honeybees: A model

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ARTICLE INFO

Article history:
Received 1 September 2009
Received in revised form 6 November 2009
Accepted 11 November 2009
Available online 11 December 2009

Keywords:
Honeybees
Thermoregulation
Division of labour
Temporal polyethism

ABSTRACT

One of the mechanisms by which honeybees regulate division of labour among their colony members is age polyethism. Here the younger bees perform in-hive tasks such as heating and the older ones carry out tasks outside the hive such as foraging. Recently it has been shown that the higher developmental temperatures of the brood, which occur in the centre of the brood nest, reduce the age at which individuals start to forage once they are adult. It is unknown whether this effect has an impact on the survival of the colony. The aim of this paper is to study the consequences of the temperature gradient on the colony survival in a model on the basis of empirical data.

We created a deterministic simulation of a honeybee colony (*Apis mellifera*) which we tuned to our empirical data. In the model in-hive bees regulate the temperature of the brood nest by their heating activities. These temperatures determine the age of first foraging in the newly emerging bees and thus the number of in-hive bees present in the colony. The results of the model show that variation in the onset of foraging due to the different developmental temperatures has little impact on the population dynamics and on the absolute number of bees heating the nest unless we increase this effect by several times to unrealistic values, where individuals start foraging up to 10 days earlier or later. Rather than on variation in the onset of foraging due to the temperature gradient it appears that the survival of the colony depends on a minimal number of bees available for heating at the beginning of the simulation.

1. Introduction

Eusocial insects are characterised by a highly sophisticated division of labour among the members of the colony (Robinson, 1992). In honeybees (*Apis mellifera*), a worker performs different tasks at different ages, starting with in-hive activities like cell cleaning and brood care and ending with foraging outside the hive (Rösch, 1925). This division of labour is called temporal polyethism. The behavioural development of worker bees may be accelerated or retarded due to environmental conditions and intranidal requirements caused for example by changes in the colony age structure (Robinson, 2002; Johnson, 2003).

This behaviour appears to be highly adaptive and plastic because even under extreme environmental variation it results in homeostatic conditions. The collective organization of homeostasis is best illustrated by the colony's ability to regulate the temperature in the hive (Jones and Oldroyd, 2007), which is essential for rearing larvae and pupae. Rearing requires brood temperatures within the narrow range of 32–36 °C with a mean of 34.5 °C (Hess, 1926; Himmer, 1927; Kronenberg and Heller, 1982). Deviations from this narrow range cause serious malformations in the adult bees. To cool the hive, workers start fanning, evaporate water by tongue lashing or spread droplets of water on the brood, a behaviour that also affects humidity and CO_2 concentration of the air (Lindauer, 1954; Lensky, 1964; Seeley, 1974; Human et al., 2006). Heat is generated metabolically by "shivering" of the flight muscles (Esch, 1960; Harrison, 1987; Kleinhenz et al., 2003). Furthermore, workers can regulate the colony temperature by clustering tightly together. Tightening of the cluster reduces thermal conductance and increases thermal insulation, whereas loosening of the cluster facilitates the cooling of the nest (Owens, 1971; Severson and Erickson, 1990; Stabentheiner et al., 2003). The more workers are available, the bigger the cluster can be, and the larger is the size of the heated region in the colony. As the colony size strongly increases in spring, the differences in the numbers of workers over the season will have a significant influence on the temperature of the brood nest.

The importance of temperature regulation is pervasive. Higher temperatures during their pupal development lead to an increased dancing activity, to better memory in adults (Tautz et al., 2003; Groh et al., 2004), and to a faster behavioural and physiological development, which results in precocious foraging (Becher et al., 2009). This in turn influences the number of bees that are present in the colony during daytime: colonies with higher brood nest temperatures will have reduced numbers of in-hive bees because workers develop

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doi:10.1016/j.ecolmodel.2009.11.016

into foragers earlier. A reduced number of in-hive workers in turn will have negative effects on the size and temperature of the brood nest, as only a limited number of larvae can be fed and incubated by each nurse bee. Cooler developmental temperatures however will then extend the in-hive period of the emerging workers and hence increase the number of workers available for heating the nest. Thus, we hypothesise that the variance in the onset of foraging, caused by differences in the developmental temperature, strongly affects the population dynamics and the survival of the colony.

We study this interplay between brood nest size, brood nest temperature and the duration of the in-hive period with a deterministic model that combines the empirical temperature profiles in the brood nest with colony dynamics. We tuned the model with our own empirical data of the temperature distribution on brood combs and of the heat production of foragers and in-hive bees under various group sizes. In the first part of this article we describe the empirical results of temperature measurements. In the second part, we present the model and its results.

2. Empirical data

2.1. Methods

2.1.1. Natural temperature distribution on a brood comb

To analyse the temperature distribution on a brood comb we constructed a measurement device with 256 sensors. We recorded one sensor after the other every second, so each complete temperature record lasted 256 s (Becher and Moritz, 2009). The sensors were placed on a 15 cm × 15 cm area and touched the bottom of the cells at the backside of the test comb. The temperature measurement took place in a standard honeybee colony (*A. mellifera*). The colony contained four frames with about 3000 workers and a laying queen. It was kept at room temperature (25 °C) in the laboratory, with a flight entrance connecting to the outside. The queen readily laid eggs in the test comb, and size and position of the brood nest was verified at the end of the experiments. As workers had access only to one side of the comb, temperatures were about 1.5 °C lower than under natural conditions.

2.1.2. Temperature gradient and number of heating bees

To determine, whether the temperature gradient, is influenced by the number of heating bees, we studied groups of various sizes (50–250 workers). In-hive bees were collected from the brood nest of a donor colony as follows.

We brushed bees in the daylight from a brood comb to the ground. Whereas older bees flew up, younger in-hive bees showing a negative phototactic behaviour were crawling in a dark box provided to the bees. Only those young bees were used for the experiments.

The in-hive bees were confined to the 15 cm × 15 cm area of the empty test comb, where the temperature measurement took place. A square piece of capped brood containing either 100 or 200 cells was inserted into the centre of the comb. We recorded the temperature distribution for 20 h. The temperature gradient was calculated as the temperature difference between the hottest and coldest sensor in the brood area, divided by the distance of these sensors, averaged over the last 30 time steps (2 h 08 min).

2.1.3. Contribution of foragers and in-hive bees to the brood temperature

To test for differences in the heat production by foragers and in-hive bees, we used a similar experimental setup as described for the analysis of the temperature gradient. Groups of 150 bees from a donor colony either collected at the flight entrance (foragers) or from the brood nest using negative phototactic behaviour (in-hive bees), were confined on the test comb of our temperature measurement instrument. Heat production was measured on a piece of capped brood (100 cells). Experiments took place at 25 °C ambient temperature and lasted for 10 h. Bees were supplied with honey *ad libitum*.

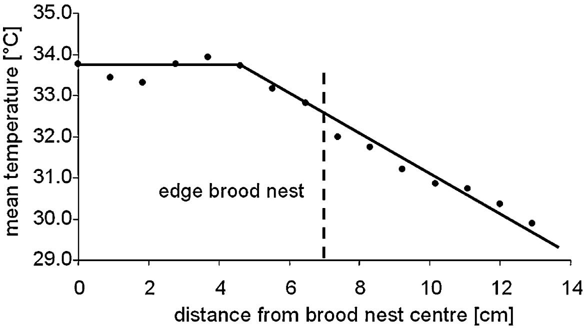

Fig. 1. Empirical temperatures along a transect through a brood nest area. Each data point contains the information of 763 temperature records (data collected between June 16th and 24th 2006 and measured in a common colony at 25 °C).

2.1.4. Heat production of in-hive bees

To determine the capability of actual heat production of a single bee, we used the experimental setup described above to study various groups of in-hive bees on 200 capped brood cells on the test comb. We studied the group at room temperature (ca. 25 °C) in the dark to reduce the disturbance of the bees. We recorded the ambient temperature as well as the position of the bees on the comb using an infrared camera. The heat, produced by single bee was calculated as

$$\text{heat per bee}\,(t) = \frac{(\text{mean broodnest}\,T(t) - \text{ambient}\,T(t)) \cdot N\,\text{broodcells}}{N\ \text{heating bees}\,(t)} \tag{1}$$

2.2. Empirical results

2.2.1. Temperature distribution on a brood comb

Fig. 1 shows the temperatures of a transect through the central brood nest. We found an even temperature distribution in the core of the brood nest. Beyond this core area, the temperature linearly decreased with a slope of 0.45 °C/cm. Brood cells were not only present in the well heated core area, but also at the cooler edge.

2.2.2. Temperature gradient and number of heating bees

We found no correlation between the size of the group and the slope of the temperature gradient (Spearman rank order—2007: $R = 0.31$, $p = 0.45$, $N = 8$; 2008: $R = 0.15$, $p = 0.73$, $N = 8$) (Fig. 2). Thus,

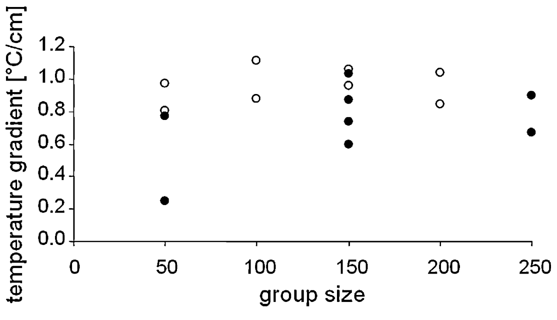

Fig. 2. Temperature gradients under experimental conditions of 100 (●) and 200 (○) brood cells.

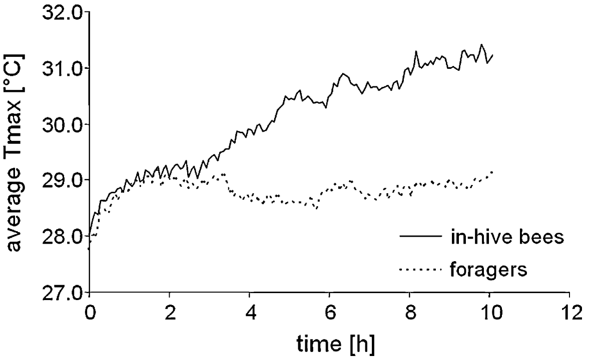

Fig. 3. Maximum temperatures on a piece of capped brood without gaps at ambient temperatures of 25 °C produced by 150 test bees ($N_{\text{In-hive}} = 4$, $N_{\text{Forager}} = 4$).

the slope of the temperature decrease at the edge of the brood nest was in our experimental setup independent of the number of bees.

2.2.3. Contribution of foragers and in-hive bees

Compared to foragers in-hive bees showed a significantly higher heat production resulting in in-hive temperatures above 31 °C (Whitney–Mann *U*-test: $p = 0.04$, $N_{\text{In-hive}} = 4$, $N_{\text{Forager}} = 4$). Foragers maintained the brood nest temperature between 28 °C and 29 °C (Fig. 3).

2.2.4. Heat production of in-hive bees

We calculated that a single bee could increase the temperature in a single cell by 26.5 °C. This temperature increase was reached within 6 h and then held constant for another 6 h (Fig. 4). We conclude that the heat production of a single bee allows her to raise the temperature of 2.65 cells by 10 °C. These 10 °C reflect the temperature difference in the model between the ambient temperature (25 °C) and the optimal temperature (35 °C). Thus a single heater bee in the model is able to maintain the optimal nest temperature for 2.65 brood cells.

3. The model

3.1. General description of the model

The model represents the dynamics of a colony on a single brood comb of an unlimited size. We assume three distinct life phases of every worker bee: the brood phase lasting 21 days, the in-hive phase of 15 days and the foraging phase of 10 days. The number of individuals at the first day of the brood phase equals the number of eggs being laid by the queen. During each time step all individuals age 1 day and at the end of the foraging period, they die. The temperature distribution in the brood nest is determined by the total number of heating bees and by the number of brood cells. Brood nest temperatures are recorded in the model and determine the proportion of hot, medium tempered and cold bees at emergence. We give bees that develop in cells with a mean temperature below a certain threshold (so-called 'cold' bees) a prolonged in-hive period, those in cells with a temperature above this threshold (called 'medium tempered bees') a normal onset of foraging and 10% of the medium tempered bees (so-called 'hot bees') we induce to forage precociously (Table 1).

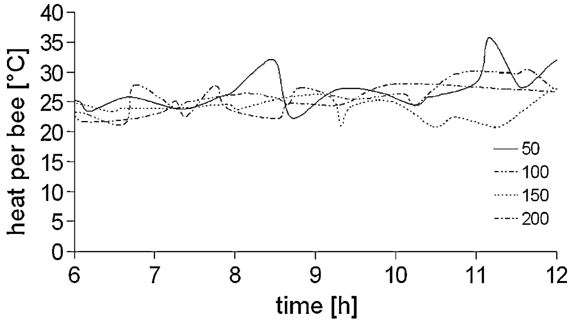

Fig. 4. Empirical heat production by a single worker on a piece of capped brood in groups of 50–200 bees. Each data series represents the average values of two replicates.

Table 1
Model constants.

Name	Value
MAX_EGGLAYING_RATE	1500 eggs/day
CELLSIZE	0.25 cm^2
T_HOT	36 °C
T_OPTIMAL	35 °C
T_COLD	33 °C
T_EDGE	32 °C
T_FREEZING	31 °C
TEMP_GRADIENT	0.45 °C/cm (standard value)
MAX_HEATEDCELLS_PER_BEE	2.65 cells (standard value)

3.2. Initial colony situation

The comb is represented in the model as an unlimited, two-dimensional plane with brood on one side only. The colony starts without brood with N_INITIAL WINTERBEES. The WINTERBEES represent those that overwintered and which are characterised by a very long lifespan. They do not develop further but they perform both the task of brood heating as well as foraging (not explicitly included into the model). These WINTERBEES die at a constant rate within 100 days.

$$\begin{aligned} &\textbf{if } t \le \textbf{100 then } \text{N\_WINTERBEES}(t) = \text{N\_INITIAL} - \text{round}\left(\frac{t \cdot \text{N\_INITIAL}}{100}\right) \\ &\textbf{if } t > \textbf{100 then } \text{N\_WINTERBEES}(t) = 0 \end{aligned} \tag{2}$$

3.3. The temperature distribution

The temperature distribution on the comb depends on the number of heating bees ('HEATERS'):

$$\text{N\_HEATERS}(t) = \text{N\_WINTERBEES}(t) + \text{TOTAL\_INHIVE\_BEES}(t) \tag{3}$$

We assume that the temperature in the core of the brood nest is uniform and constant at T_OPTIMAL of 35 °C. The maximum number of brood cells at T_OPTIMAL (the so-called MAX_OPTHEAT_CELLS) depends on the number of bees that heat, and their maximal heating abilities:

$$\begin{aligned} &\text{MAX\_OPTHEAT\_CELLS}(t) \\ &\quad = \text{N\_HEATERS}(t) \cdot \text{MAX\_HEATEDCELLS\_PER\_BEE} \end{aligned} \tag{4}$$

Beyond this area at T_OPTIMAL, the temperature decreases linearly following the parameter TEMP_GRADIENT (°C/cm) as observed in the empirical data.

HEATERS reduce the actual number of heated brood cells to the minimum, which means, that only the brood nest and empty cells for the subsequent egg laying are heated properly. Hence, as long as the brood nest temperature is not limited by the maximal heating abilities of the heating bees, the area with a temperature ≥ T_EDGE (32 °C) contains N_BROODCELLS brood cells and some empty cells. These empty cells are necessary for a continuous egg laying, as the queen lays eggs only in cells with a temperature of at least 32 °C. The number of these empty cells equals the maximum number of eggs that can be laid by the queen on 1 day (= MAX_EGGLAYING_RATE). It is set to 1500 eggs/day. Given that there are enough HEATERS to generate the required temperatures we calculate the actual number of cells with a temperature of T_OPTIMAL (35 °C) in a way that the above condition is fulfilled. The number of optimally heated cells is represented by the parameter N_OPTHEAT_CELLS(t). This method ensures, that always some brood cells have temperatures below the optimum, even if the colony is large in relation to the brood nest.

3.4. Hot, cold, and medium tempered brood

We calculate the radius of the optimally tempered core region of the brood nest as follows:

$$\text{RADIUS\_OPT\_T}(t) = \left(\frac{\text{N\_OPTHEAT\_CELLS}(t) \cdot \text{CELLSIZE}}{\pi}\right)^{1/2} \tag{5}$$

The radius of medium tempered area, i.e. the area where the brood temperature is higher than the T_COLD threshold is then calculated as:

$$\text{RADIUS\_MEDIUM\_T}(t) = \text{RADIUS\_OPT\_T}(t) + \frac{\text{T\_OPTIMAL-T\_COLD}}{\text{TEMP\_GRADIENT}} \tag{6}$$

with TEMP_GRADIENT as the slope of the linear temperature decrease beyond the optimally heated area, set to 0.45 °C/cm.

This allows us to calculate the number of the medium tempered and cold broodcells:

$$\text{N\_MEDIUM\_T\_CELLS}(t) = \frac{\pi \cdot (\text{RADIUS\_MEDIUM\_T}(t))^2}{\text{CELLSIZE}} \tag{7}$$

$$\text{N\_COLD\_T\_CELLS}(t) = \text{N\_BROODCELLS}(t) - \text{N\_MEDIUM\_T\_CELLS}(t) \tag{8}$$

3.5. Egg laying and brood nest

The number of new eggs laid per day is determined by the maximal egg laying rate (1500 eggs/day) and the number of empty brood cells in the potential brood nest, i.e. the area with a temperature ≥ T_EDGE (32 °C).

$$\text{EMPTY\_CELLS}(t) = \frac{\pi \cdot (\text{RADIUS\_T\_EDGE}(t)^2)}{\text{CELLSIZE}} - \text{N\_BROODCELLS}(t) \tag{9}$$

RADIUS_T_EDGE(t) is the radius of the T_EDGE isotherm (32 °C). Then the number of new laid eggs at time step t is:

$$\begin{array}{l} \text{NEW\_EGGS}(t) = \text{EMPTY\_CELLS}(t) \\ \textbf{if } \text{NEW\_EGGS}(t) > 1500 \textbf{ then } \text{NEW\_EGGS}(t) = 1500 \\ \textbf{if } \text{NEW\_EGGS}(t) < 0 \textbf{ then } \text{NEW\_EGGS}(t) = 0 \end{array} \tag{10}$$

The number of brood cells is calculated as follows:

$$\begin{array}{ll} \textbf{for } t = 1: & \text{N\_BROODCELLS}(t) = \text{NEW\_EGGS}(t) \\ \textbf{for } t > 1: & \text{N\_BROODCELLS}(t) = \text{N\_BROODCELLS}(t-1) + \text{NEW\_EGGS}(t) - \text{FROZEN\_EGGS}(t) - \text{EMERGED\_allT}(t) \end{array} \tag{11}$$

FROZEN_EGGS may occur, if the number of HEATERS decreases due to the dying of WINTERBEES or because too many INHIVE_BEES developed into foragers. If the temperature at the edge of the brood nest falls below the critical threshold T_FREEZING (31 °C), then brood cells will be lost due to freezing. N_FROZEN_EGGS(t) is then calculated as:

$$\text{N\_FROZEN\_EGGS}(t) = \frac{\pi \cdot (\text{RADIUS\_BROODNEST}(t)^2 - \text{RADIUS\_T\_FREEZING}(t)^2)}{\text{CELLSIZE}} \tag{12}$$

RADIUS_BROODNEST(t) is the radius of the brood nest and RADIUS_T_FREEZING(t) is the radius of the T_FREEZING isotherm (31 °C) in time step t. The number of frozen brood is subtracted from N_BROOD(age,t), starting with the youngest age cohorts.

3.6. Brood development and emergence

The number of brood at a given age is calculated as:

$$\begin{array}{ll} \textbf{for age} = \textbf{1}: & \text{N\_BROOD}(age, t) = \text{NEW\_EGGS}(t) \\ \textbf{for 1} < \textbf{age} < \textbf{21}: & \text{N\_BROOD}(age, t) = \text{N\_BROOD}(age-1, t-1) \\ \textbf{for age} = \textbf{21}: & \text{N\_BROOD}(age, t) = 0 \end{array} \tag{13}$$

The number of newly emerged INHIVE_BEES is computed from the number of brood in the oldest brood cohort:

$$\text{EMERGED\_allT}(t) = \text{N\_BROOD}(age = 20, t-1) \tag{14}$$

3.7. The developmental temperature

To determine the proportion of INHIVE_BEES developed under hot, medium, or cold conditions, the proportion of medium tempered and cold brood cells in each time step is averaged over the complete brood development period, resulting in the parameter PROP_MEDIUM_DEV_T. As the model does not provide temperatures above the T_OPTIMAL (35 °C), we derive the number of hot cells from the number of cells with optimal temperature. We make 10% of the N_MEDIUM_T_CELLS(t) into “hot” cells of 36 °C.

$$\text{PROP\_MEDIUM\_DEV\_T}(t) = \frac{\sum_t^{t-21} \text{N\_MEDIUM\_T\_CELLS}(t)}{\sum_t^{t-21} \text{N\_MEDIUM\_T\_CELLS}(t) + \sum_t^{t-21} \text{N\_COLD\_T\_CELLS}(t)} \tag{15}$$

The number of newly emerged medium tempered INHIVE_BEES is then:

$$\text{EMERGED\_medium}(t) = \text{round}(\text{EMERGED\_allT}(t) \cdot \text{PROP\_MEDIUM\_DEV\_T}(t) \cdot 0.9) \tag{16}$$

Only 90% of the N_MEDIUM_T_CELLS(t) contribute to the new emerged medium tempered INHIVE_BEES. The remaining 10% of the N_MEDIUM_T_CELLS(t) are assumed to be “hot” (36 °C).

$$\text{EMERGED\_hot}(t) = \text{round}(\text{EMERGED\_allT}(t) \cdot \text{PROP\_MEDIUM\_DEV\_T}(t) \cdot 0.1) \tag{17}$$

$$\text{EMERGED\_cold}(t) = \text{EMERGED\_allT}(t) - \text{EMERGED\_medium}(t) - \text{EMERGED\_hot}(t) \tag{18}$$

3.8. Behavioural development of the adult bees

In the absence of a temperature effect on the behavioural development, the number of INHIVE_BEES is calculated as follows, with a maximum age of 15 days:

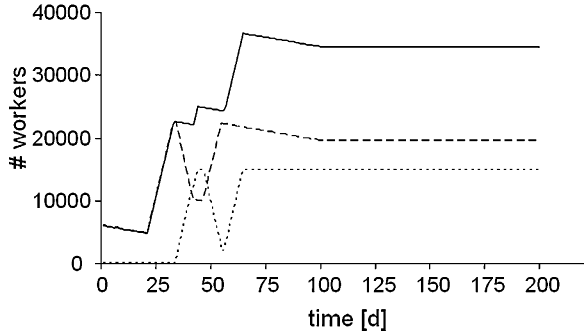

Fig. 5. Colony dynamics in the model starting with 6000 initial bees. The number of in-hive bees including initial bees (dashed line), the number of foragers (dotted line) and the total number of all workers (continuous line) are shown for the parameter set at default values (TEMP_GRADIENT = 0.45, MAX_HEATEDCELLS_PER_BEE = 2.65, TempEff = 0).

$$\begin{array}{ll} \textbf{for age} = \mathbf{1}: & \text{N\_INHIVE\_BEES}(age, t) = \text{EMERGED\_allT}(t) \\ \textbf{for } \mathbf{1} < \textbf{age} < \mathbf{15}: & \text{N\_INHIVE\_BEES}(age, t) = \text{N\_INHIVE\_BEES}(age - 1, t - 1) \end{array} \tag{19}$$

The total number of all INHIVE_BEES is hence the summed number of INHIVE_BEES over all age cohorts:

$$\text{TOTAL\_INHIVE\_BEES}(t) = \sum_{age=1}^{age=15} \text{N\_INHIVE\_BEES}(age, t) \tag{20}$$

The number of FORAGERS is calculated on the basis of the oldest in-hive bees cohort:

$$\begin{array}{ll} \textbf{for age} < \mathbf{15}: & \text{N\_FORAGERS}(age, t) = 0 \\ \textbf{for age} = \mathbf{15}: & \text{N\_FORAGERS}(age, t) = \text{N\_INHIVE\_BEES}(age - 1, t - 1) \\ \textbf{for } \mathbf{15} < \textbf{age} < \mathbf{25}: & \text{N\_FORAGERS}(age, t) = \text{N\_FORAGERS}(age - 1, t - 1) \\ \textbf{for age} = \mathbf{25}: & \text{N\_FORAGERS}(age, t) = 0 \end{array} \tag{21}$$

3.9. Influence of the temperature effect on population dynamics

If we include in the model the effect of brood temperature on the behavioural development, the in-hive period is no longer fixed at 15 days but depends on the mean brood temperature an individual was exposed to during its development. The parameter TEMP_EFFECT describes the strength of this temperature effect. A value of zero means no influence of brood temperature (i.e. the same duration of in-hive period for all bees, irrespective of their developmental temperature). A value of one reflects a 1 day shorting of the in-hive period for hot bees and a prolongation by 1 day for cold bees, a value of two reduces the in-hive period of hot bees by 2 days and prolongs it for cold bees by 2 days, etc.

$$\begin{array}{ll} \textbf{for age} = -\textbf{TEMP}\text{\_EFFECT} + \mathbf{1}: & \text{N\_INHIVE}(age, t) = \text{N\_INHIVE}(age - 1, t - 1) + \text{EMERGED\_cold}(t) \\ \textbf{for age} = \mathbf{1}: & \text{N\_INHIVE}(age, t) = \text{N\_INHIVE}(age - 1, t - 1) + \text{EMERGED\_medium}(t) \\ \textbf{for age} = \textbf{TEMP}\text{\_EFFECT} + \mathbf{1}: & \text{N\_INHIVE}(age, t) = \text{N\_INHIVE\_BEES}(age - 1, t - 1) + \text{EMERGED\_hot}(t) \\ \textbf{for age} < \mathbf{15} \textbf{ and age} \notin \{(-\textbf{TEMP}\text{\_EFFECT} + \mathbf{1}), \mathbf{1}, (\textbf{TEMP}\text{\_EFFECT} + \mathbf{1})\}: & \text{N\_INHIVE\_BEES}(age, t) = \text{N\_INHIVE\_BEES}(age - 1, t - 1) \\ \textbf{for age} < (-\textbf{TEMP}\text{\_EFFECT} + \mathbf{1}) \textbf{ or age} \geq \mathbf{15}: & \text{N\_INHIVE\_BEES}(age, t) = 0 \end{array} \tag{22}$$

4. Model results

4.1. Colony dynamics

The colony dynamics show strong fluctuations in the number of INHIVE_BEES (Fig. 5). These fluctuations occur, because the queen stops egg laying when no empty cells with a suitable temperature are available. The same pattern repeats itself in the foragers 10 days later. The linear decrease of the colony size in the beginning and after the maximal colony size is reached reflects the continuous loss of WINTERBEES. After 21 days, when the first adults emerge, the colony starts growing. The colony size reaches a steady state, when the number of new emerged INHIVE_BEES per day equals the maximal egg laying rate of the queen. When we increase the maximal egg laying rate of the queen (from 1000 to 2000 eggs/day), this results in proportionally increased colony sizes in the steady state.

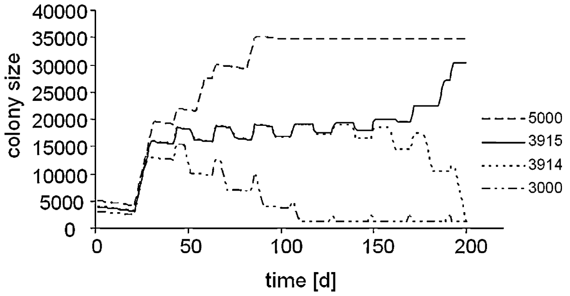

Fig. 6. The model dynamics of colony size (number of workers) for different numbers of initial bees (3000, 3914, 3915 and 5000) at default values (TEMP_GRADIENT = 0.45, MAX_HEATEDCELLS_PER_BEE = 2.65, TempEff = 0).

4.2. Impact of initial colony size

The survival of a colony depends on the initial number of WINTERBEES (Fig. 6). The colony size will only increase, if enough new workers emerge and hence if the number of available brood cells is high enough. This directly depends on the initial number of WINTERBEES. Under the empirically based parameter set (TEMP_GRADIENT = 0.45, MAX_HEATEDCELLS_PER_BEE = 2.65) without temperature effect (TempEff = 0), we find that a minimal number of 3915 initial bees is required for colony survival. We call this value the "survival threshold", the minimum number of initial bees to ensure colony survival. If this survival threshold is undershot by the initial number of WINTERBEES, the colony is doomed to die. The number of HEATERS in such a colony is too small to provide sufficient heat for a brood nest, that is large enough to maintain the colony size, even if there may temporarily be nearly 20,000 individuals present. Reducing the maximal egg laying rate to 1000 eggs/day decreases the survival threshold to 2283 bees whereas increasing it to 2000 eggs/day increases the survival threshold to 5640 bees.

4.3. Influence of the temperature effect

If we include the temperature effect in the simulation, leading to a prolonged in-hive period for cold bees (16 d) and a shorter in-hive period for hot bees (14 d), we find a reduction in the survival threshold of 27 individuals to 3888 initial bees. By increasing the impact of the temperature effect, we further reduce the minimal number of initial bees, needed for the colony survival (Fig. 7).

4.4. Structure of the parameter space

The survival threshold decreases when more cells are heated per HEATER and when the temperature decrease at the edge of the nest

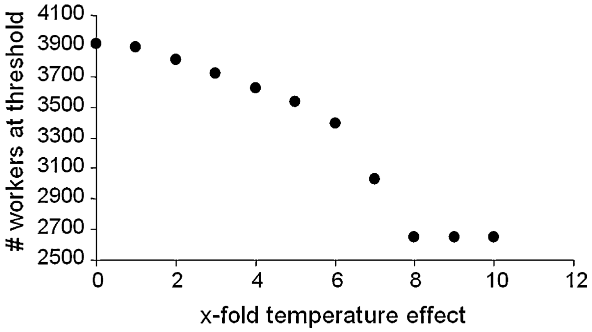

Fig. 7. Survival thresholds (i.e. minimal number of initial bees needed for colony survival) in the model in relation to the temperature effect (0: no temperature effect, 1: empirical temperature effect, >1: accordingly magnified temperature effect) (TEMP_GRADIENT = 0.45, MAX_HEATEDCELLS_PER_BEE = 2.65).

is low, so that temperature gradient is flat (Fig. 8). To assess the relation between costs for heating the brood and benefits by a reduction of the colonies survival threshold, we used the parameter "relative gain", calculated as the percental decrease of the survival thresholds divided by the percental increase of the number of heated cells (respectively the slope of the temperature gradient) when moving through the parameter space (Figs. 9 and 10). As long as the relative gain is above one, it should pay for the colony to increase the heating effort.

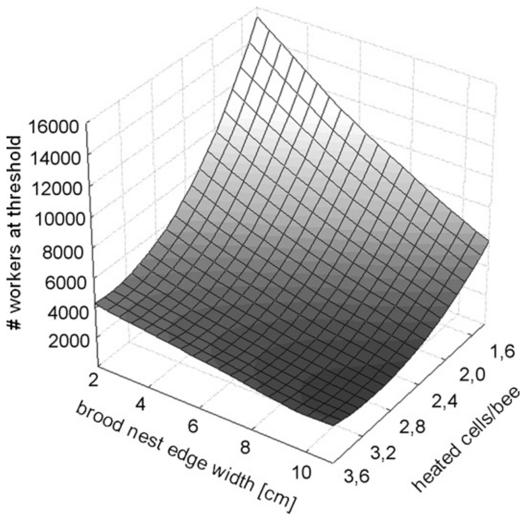

Fig. 8. Survival thresholds (i.e. minimal number of initial bees for colony survival) in relation to the width of the edge of the brood nest (≤35 °C) and the number of heated cells per bee (TempEff = 0).

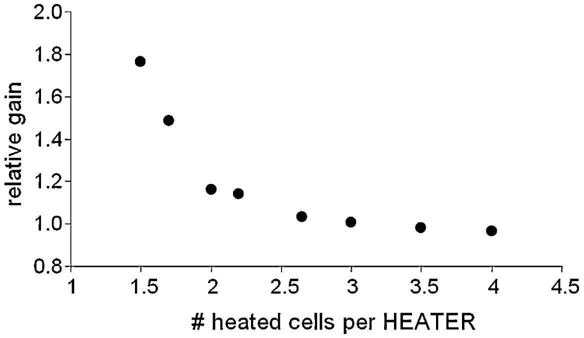

Fig. 9. The relative gain for different numbers of heated cells per heater. The relative gain is derived from benefits of enhanced survival in relation to the additional costs on increased heating per bee. Thus the relative decrease of number of bees at the survival threshold is divided by the relative increase in heating effort (TEMP_GRADIENT = 0.45).

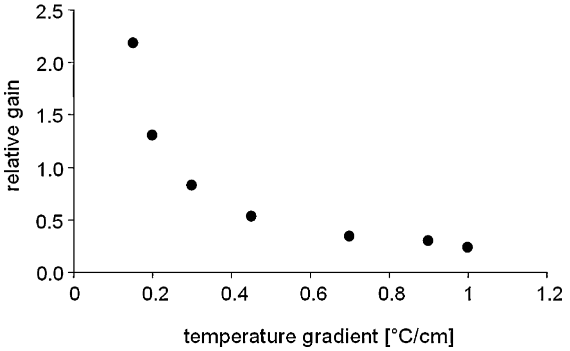

Fig. 10. The relative gain versus the temperature gradient. The relative gain is derived from benefits of enhanced survival in relation to the additional costs on a flattened temperature gradient. Thus the relative decrease of number of bees at the survival threshold is divided by the relative decrease of the temperature gradient (heat per bee = 26.5 °C).

5. Discussion

5.1. Model assumptions

To implement the brood nest temperature in the model we used the data from literature (Himmer, 1927; Kronenberg and Heller, 1982) rather than our own slightly lower empirical data because bees were only able to heat on one side of the comb in our experiment. The values for the temperature gradient (TEMP_GRADIENT = 0.45), derived from the colony experiment is lower, than those, measured under the artificial conditions with small group sizes (Fig. 2). Since we estimated the temperature gradient for the experiments with small group sizes, as the temperature difference between the hottest and the coldest cell the value does no reflect the mean but the maximum temperature gradient. We therefore used the values derived from the colony measurements also because they are based on a more extensive data set (763 temperature records within 8 days) recorded under the nearly natural conditions, reflecting the mean temperature gradient. Our estimate was very close to the temperature gradient derived from a diffusion model of a honeybee swarm by Myerscough (1993) with a temperature decrease of 0.46 °C/cm with 5000 bees at 25 °C ambient temperature.

We found no correlation between the number of heating bees and the temperature gradient at the edge of the brood nest (Fig. 2), hence the colony size does not seem to influence the slope of the temperature decrease beyond the core brood nest.

As in-hive bees produced much higher brood temperatures than foragers (Fig. 3), the brood nest temperature in the model is determined by the INHIVE_BEES and the WINTERBEES, but not by the FORAGERS. Moreover, in reality foragers are usually located on the periphery of the combs or close to the flight entrance, but not near to the brood and hence are less involved in heating the brood.

The contribution of a single bee to the thermal profile of the brood nest was not influenced by the group size. We assume that the measured value of 26.5 °C per bee represents the maximal heating capability of the bees, since the temperatures on the brood piece were always far below the optimal temperatures of 35 °C.

5.2. Model results

5.2.1. Colony dynamics

Although we simulated extremely artificial conditions the results match the absolute size and dynamics of real honeybee colonies well. If we assume that the first time step in the model represents initial egg laying in mid February, then a colony starting with 6000 winter bees would peak in the mid of April (∼t = 60), which is close to the actual swarming time of natural colonies in late April and early May (Winston, 1980). The maximum colony size in the model is about 37,000 WORKERS. Imdorf et al. (1996) report of maximum colony sizes ranging from about 18,000 to about 35,000 workers, but clearly also much larger colonies with more than 60,000 workers can occur in apicultural operations (Farrer, 1937). Schmickl and Crailsheim (2007) present maximum colony sizes of 30,000–50,000 bees in their honeybee population model. While colony size naturally depends on a multitude of environmental and intracolonial factors, the equilibrium colony size in the model depends mainly on the maximum egg laying rate of the queen. Winston et al. (1981) show the average colony dynamics of three Africanized and European honeybee colonies, starting with ca. 16,000 workers. After 20 days, when the first brood emerges the colonies have lost about 50% of the workers and after 65 days the colony sizes reach the maximum with 20,000–25,000 workers.

5.2.2. *Initial colony size*

According to our model a minimum colony size of 3915 WINTERBEES at the beginning of the simulation was required to ensure the survival of the colony. This resembles empirical data. For instance, beekeepers in Central Europe suggest minimal colony sizes in autumn of 5000–7500 workers. Colony sizes in spring are about 75% of the autumn colony sizes (Rosenkranz, 2008), which results in about 3750–5625 workers for small colonies. Note that these values are probably higher than the minimum colony sizes to avoid colony losses for the beekeepers. Winston (1980) presents data from swarming colonies, with minimum swarm sizes of 3765 individuals and of 3200 in Lee and Winston (1985). The increase of the survival thresholds when the maximal egg laying rate increases seems to be counterintuitive, but can be explained by amplified fluctuations in the number of in-hive bees. A sudden decrease in the number of HEATERS, when a large cohort of IN-HIVE BEES develops into FORAGERS can result in cooling of the brood with lethal consequences for the colony . In reality, a slow increase of the egg laying rate during spring is observed (Allen, 1960). Our model suggests that this slow increase of the egg laying rate in empirical data may not only be due to constraints but may also be adaptive because it smoothens the colony growth.

5.2.3. *Temperature effect*

The shortened duration of the in-hive period due to high developmental temperature had a nearly negligible influence on the resulting survival thresholds under the empirical parameter set. It reduced the minimum number of initial WINTERBEES necessary for colony survival by only 27 individuals or 0.4%. Therefore, it will have only limited impact on the organization of the overall colony structure. Reducing the proportion of hot bees, fixed in the model to 10% of the medium tempered bees, would gently decrease the survival threshold of the colony, as then more in-hive bees were available due to the later onset of foraging in the cold and medium tempered bees. Increasing the temperature effect more than eightfold leads to a strong variation of age of first foraging but does not decrease the survival threshold any further. This is caused by an overlapping of the generations of in-hive bees. For such large values of the temperature effect (i.e. ≥ 8), the in-hive period of bees developed under cold brood temperatures becomes longer than the duration of the development from egg to the adult bees. This strongly increases the number of in-hive bees present in the colony and guarantees a continuous egg laying.

5.2.4. *Parameter space*

The survival threshold decreases with increasing number of heated cells per HEATER and with a decreasing slope of the temperature gradient. A larger number of heated cells increases the core region of the brood nest whereas a flattened temperature gradient increases the 32–35 °C area of the brood nest. Hence, more eggs can be laid and more INHIVE_BEES will emerge to further increase the brood nest size. However, heat production is costly and the realized temperature distribution will be a result of a trade-off between the benefits of a stronger colony growth and the costs of higher energy expenditure. We did neither include heating costs nor energy income by foraging into the model, but we tried to assess the “relative gain” of the colony. This is the percentage decrease of the survival threshold divided by the increase of the number of heated cells (respectively the slope of the temperature gradient) when moving through the parameter space. If the number of heated cells per HEATER is below 2.5, then the relative gain (for TEMP_GRADIENT = 0.45, Fig. 9) is clearly above one and hence it should be beneficial for the colony to further increase the heating efforts. The empirical value of 2.65 heated cells per bee the relative gain is close to one hence a further increase in the number of heated cells may seem not efficient.

Analysing the relative gain for 2.65 heated cells per HEATER, we should expect a temperature gradient of about 0.27 °C/cm. This is lower than the empirical value of 0.45 °C/cm.

6. Conclusions

Our model is based on very simple assumptions and does not intend to imitate the complex processes of a natural colony and its manifold interactions with the environment. Instead it focuses on the relation between colony size and temperature distribution in the brood nest. In real colonies, eggs are laid on both sides of the comb, and hence the bees can raise twice as much brood as in the model, with only little more heating effort. Usually the brood nest is distributed over several combs. If the same amount of brood is subdivided into several parts distributed over many combs, then the proportion of cells at the edge and hence the proportion of cold brood will be higher. This would possibly increase the influence of the temperature effect. On the other hand, the three-dimensional structure of a honeybee cluster on a real brood nest provides a higher insulation and an increased utilization of the produced heat resulting in more warm cells and reducing multiple edge effects. In any case, since the enhancing of the temperature effect by an order of magnitude well beyond the biological limits did not substantially change our results, it seems that the temperature effect can only have a limited impact on the organization of the division of labour in real colonies, even if the proportion of cold bees in real colonies would deviate from the proportions in our model. Instead, the absolute number of bees available for the heating and nursing processes seems to be the critical factor determining the thriving and survival of the colony.

Acknowledgements

We thank Julia Schröder, Martin Hinsch, Daan Reid and the other members of the Theoretical Biology Group in Groningen for helpful discussions, and all students involved in the record of empirical data (Nadine Hartmann, Judith Kreher, Juliane Mohr, Katja Schönefeld, Stefanie Stöckhardt, Anne Blaner, Christiane Hösel, Anne-Katrin Schwiderke, Alexandra Wölk). We further thank the Deutsche Forschungsgemeinschaft (RFAM) and the European Science Foundation (MAB) for funding.

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