

Caps and gaps: a computer model for studies on brood incubation strategies in honeybees (*Apis mellifera carnica*)

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Abstract In addition to heat production on the comb surface, honeybee workers frequently visit open cells (“gaps”) that are scattered throughout the sealed brood area, and enter them to incubate adjacent brood cells. We examined the efficiency of this heating strategy under different environmental conditions and for gap proportions from 0 to 50%. For gap proportions from 4 to 10%, which are common to healthy colonies, we find a significant reduction in the incubation time per brood cell to maintain the correct temperature. The savings make up 18 to 37% of the time, which would be required for this task in completely sealed brood areas without any gaps. For unnatural high proportions of gaps (>20%), which may be the result of inbreeding or indicate a poor condition of the colony, brood nest thermoregulation becomes less efficient, and the incubation time per brood cell has to increase to maintain breeding temperature. Although the presence of gaps is not essential to maintain an optimal brood nest temperature, a small number of gaps make heating more economical by reducing the time and energy that must be spent on this vital task. As the benefit depends on the availability, spatial distribution and usage of gaps by the bees, further studies need to show the extent to which these results apply to real colonies.

Keywords Honeybee · *Apis mellifera* · Brood nest · Brood gaps · Thermoregulation · Multi-agent based computer simulation

Introduction

Honeybees maintain a brood nest temperature between 33 and 36°C, which is optimal for brood development (Tautz et al. 2003; Groh et al. 2004). Specialised incubation behaviour without doing any other work is displayed by motionless worker bees (Esch 1960; Schmaranzer et al. 1988), which press their heated thorax onto the brood caps for several minutes (Bujok et al. 2002). Similar to social wasps, brood incubation is also performed by workers inside “gaps” (Kleinhenz et al. 2003), i.e. in open cells that are scattered in the sealed brood area at low rates. We investigated how heat production inside these gaps helps the colony to save energy and time, which must be spent on the regulation of brood temperature.

Materials and methods

We employed a multi-agent based computer model using the simulation tool SeSAM (Oechslein 2004; Klügl et al. 2006) to study the efficiency of brood nest incubation. The simulation model consists of two main components: a physical model of the temperature changes between comb cells (Kleinhenz et al. 2003) and a behavioural bee model including different heating strategies.

The simulated environment is an area of 20×20 hexagonal cells, consisting of sealed brood cells and distinct proportions of “gaps”, i.e. open cells (Ruttner 1996) scattered among them. The bee agents ($N=134$) have

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the task to keep the brood temperature in the optimum range.

As some gaps may be filled with food during daytime, our model is most applicable to the situations at night and in the early morning when temporary food stores next to brood are empty (Camazine 1991) and accessible to cell visitors. Eggs or young brood (before capping) may be found in these gaps but are not modelled, as their presence

is not essential to trigger heat production by cell visitors as described above.

Based on initial results, additional simulations were performed with gaps present ($n_{\text{Gaps}}=5, 10, 20\%$, $T=28^\circ\text{C}$, $N=3$ each) but not used for brood incubation by cell visitors.

Between consecutive simulation steps, the temperature of each cell changes dependent on the temperature of its six neighbour cells and the ambient air:

$$\begin{aligned} \text{Temp}_{\text{Cell}}(t) = & \text{Temp}_{\text{Cell}}(t-1) + \sum_{\text{NeighbourCell}=1}^{\text{AdjacentCells}} \left(\Delta \left(\text{Temp}_{\text{NeighbourCell}}(t-1), \text{Temp}_{\text{Cell}}(t-1) \right) \right) \\ & \times \text{Coeff}_{\text{Cell-Cell}} + \Delta \left(\text{Temp}_{\text{AmbientAir}}(t-1), \text{Temp}_{\text{Cell}}(t-1) \right) \times \text{Coeff}_{\text{Air-Cell}} \end{aligned} \quad (1)$$

where:

$\text{Temp}_{\text{Cell}}(t)$ temperature of a cell at time t
 $\text{Coeff}_{\text{Cell-Cell}}$ influence of adjacent cells on a certain cell
 $\text{Coeff}_{\text{Air-Cell}}$ influence of the ambient air on a cell's temperature

The bee agents randomly move around and perceive the temperature of each brood cell they pass. Heating behaviour is triggered by cell temperature thresholds that are set close to the limits of the optimum range for brood rearing: T_{Heat} (33.5°C) for starting and T_{Stop} (35.5°C) for stopping the heating process. For the questions we assess, it is not relevant to consider chemical or other signals from the brood.

If a brood cell's temperature is below T_{Heat} , the agent starts to incubate this cell either by crawling into an adjacent open cell (gap) and raising its thorax temperature or, if no adjacent gap is available, by heating on this brood cell's cap.

After switching to incubation behaviour, the bee agent raises its thorax temperature up to 39°C (Schmaranzer et al. 1988; Bujok et al. 2002; Kleinhenz et al. 2003) and maintains it for up to 15 min. If the brood cell temperature exceeds T_{Stop} , the agent stops heating and resumes walking around.

For heating inside cells, the empirical temperature field is reproduced with a mean accuracy of $\pm 0.08^\circ\text{C}$. Heating on the cap of a cell is modelled as:

$$\begin{aligned} \text{Temp}_{\text{Cell}}(t) = & \text{Temp}_{\text{Cell}}(t-1) + \sum_{\text{NeighbourCell}=1}^{\text{AdjacentCells}} \left(\Delta \left(\text{Temp}_{\text{NeighbourCell}}(t-1), \text{Temp}_{\text{Cell}}(t-1) \right) \right) \times \text{Coeff}_{\text{Cell-Cell}} \\ & + \Delta \left(\text{Temp}_{\text{Bee}}(t-1), \text{Temp}_{\text{Cell}}(t-1) \right) \times \text{Coeff}_{\text{Bee-Cell}} \end{aligned} \quad (2)$$

where:

$\text{Coeff}_{\text{Bee-Cell}}$ coefficient for the influence of a single bee on a cell cap on this cell's temperature
 $\text{Temp}_{\text{Bee}}(t)$ is the thorax temperature of the bee agent Bee at time step t

For heating on a brood cap, the empirical temperature field is reproduced more accurately ($\pm 0.02^\circ\text{C}$) if additional side influences on the adjacent cells, probably caused by thermal radiation from the thorax and by warming of the air around the thorax, are assumed and modelled as:

$$\begin{aligned} \text{Temp}_{\text{Cell}}(t) = & \text{Temp}_{\text{Cell}}(t-1) + \sum_{\text{NeighbourCell}=1}^{\text{AdjacentCells}} \left(\Delta \left(\text{Temp}_{\text{NeighbourCell}}(t-1), \text{Temp}_{\text{Cell}}(t-1) \right) \right) \times \text{Coeff}_{\text{Cell-Cell}} \\ & + \sum_{i=1}^{\text{NumberAdjacentBees}} \left(\Delta \left(\text{Temp}_{\text{Bee}_i}(t-1), \text{Temp}_{\text{Cell}}(t-1) \right) \right) \times \text{Coeff}_{\text{SideBee-Cell}} \end{aligned} \quad (3)$$

where:

Cell	a cell adjacent to another cell that is being incubated by a bee staying motionless on its brood cap
NumberAdjacentBees	number of bees heating on caps of other cells that are adjacent to Cell
CoeffSide _{Bee-Cell}	coefficient for side influence of a single bee on the temperature of adjacent cells

Model calibration and validation was performed using a three-step white box calibration approach (Fehler et al. 2004, 2006). The three steps are the sequential calibration of environmental temperature dispersion, dispersion between bee agents and environment and calibration of warm-up cycles of brood incubating bees. The calibrated model reproduces empirical measurements of temperature changes resulting from dispersion between a bee’s thorax and cells and between cells of different temperature (Kleinhenz et al. 2003).

The dispersion coefficients $Coeff_{Cell-Cell}$ and $Coeff_{Air-Cell}$ were calibrated to reproduce the empirical temperature data of cells adjacent to (mean deviation 0.1°C) and of cells at a distance of one cell (mean deviation 0.06°C) to the directly heated cell. Empirical data of cell temperatures are reproduced with a mean deviation of 0.05°C for the incubated cell and 0.02°C for adjacent cells. The constant

increment for the warm-up process of the thorax is calibrated as 0.3°C per second.

Experiment Setup The number of gaps in the brood nest (n_{Gaps}) was varied from 0 to 50% and was tested at two different settings for ambient air temperature ($T=28^{\circ}C$ and $31^{\circ}C$). Every simulation run comprised 10 h of real time and was repeated five times. Following the design of experiments approach (Montgomery 1997), any proportion of gaps was tested as a random distribution and as a regular distribution.

Brood heating efficiency was determined in two ways: (1) by measuring the time the bee agents spent either on brood incubation or on walking around and (2) by estimating their energy expenditure while maintaining optimum brood nest temperature. To compensate for different numbers of brood cells in trials with different values of n_{Gaps} and to allow comparison of the results, the time and energy values are given per brood cell; that is, they represent the colony’s costs per reared larva (Fig. 1).

For each bee agent, we counted the temperature values that were required to compensate its heat loss or to raise its temperature during the simulation. For reasons of simplicity, we assume a linear proportional relationship between the sum of these temperature values per bee agent and the amount of energy required. This provided us with a relative measure of the bees’ energy expenditure for brood nest heating:

$$EnergyExpenditure_{Bee} = \sum_j^{#TimeSteps} \left(BeeTemp_{ToAir_j} + BeeTemp_{ToCells_j} + BeeTempInc(Time_{j-1}, Time_j) \right) \tag{4}$$

where:

BeeTemp _{ToAir}	temperature dispersed to air
BeeTemp _{ToCells}	temperature dispersed to cells
BeeTempInc	temperature difference when thorax temperature was raised

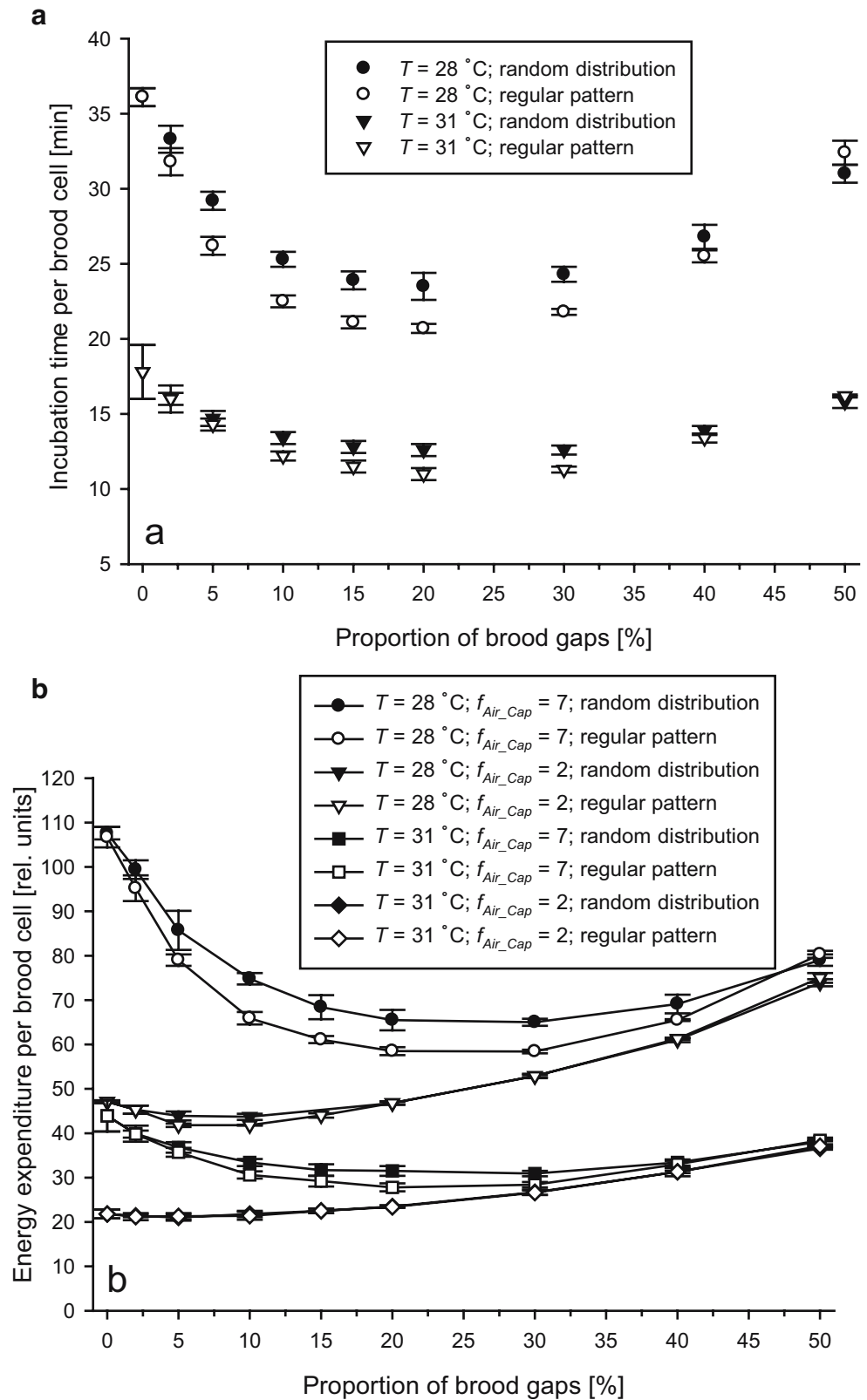
The energetic requirements of the brood comb are predetermined by the environmental settings. Additionally, heat loss from the bees to the air occurs. As all thorax surfaces except for the ventral side are exposed to the air, the cooling influence of the ambient air on a bee agent on a brood cap is larger than its influence on a bee inside a cell that has its thorax deep in the comb. To assess the influence of the ambient air’s cooling effect on the evaluation measure, we introduced two factors modelling the strength of the air’s cooling influence on bee agents visiting cells (f_{Air_Cell}) and heating on the brood caps (f_{Air_Cap}). Two

essentially different values of f_{Air_Cap} , representing almost the same influence as f_{Air_Cell} and significantly stronger influence, were tested (two and seven times higher than f_{Air_Cell}). The basic value of f_{Air_Cell} was chosen as 1, as only the position of the quantitative optimum and its gradient, but not the actual values of $EnergyExpenditure$, were of interest in our experiments.

Results

At any given set of simulation parameters (Fig. 1), a raise of the number of gaps from 0% up to a certain optimum point increases the efficiency of brood incubation both in terms of incubation time and energy expenditure per brood cell. A strictly regular gap distribution is not essential, although it may increase the benefit in comparison to

Fig. 1 Efficiency of brood incubation under different ambient conditions and with different proportions of brood gaps (mean values and SD of five trials each). Spatial distribution of gaps may be random or regular. **a** Average incubation time per brood cell during the whole simulation. **b** Evaluation measure of energy expenditure per brood cell, shown for different cooling influences of the air (see text for details). Symbols are connected by lines for better visualisation of the curves (the two lower curves for $T=31^{\circ}\text{C}$ and $f_{\text{Air_Cap}}=2$ are hardly distinguishable)



random distributions (Fig. 1) that are more likely to occur in real colonies. For high values of n_{Gaps} beyond the optimum point, the benefit declines, and time and energy requirements per brood cell increase.

The proportion of time spent on heating inside gaps and on the brood caps is given in Fig. 2. The average incubation time per brood cell decreases (Fig. 1a) if n_{Gaps} increases from 0 to 20%. Differences to the initial values ($n_{\text{Gaps}}=0\%$)

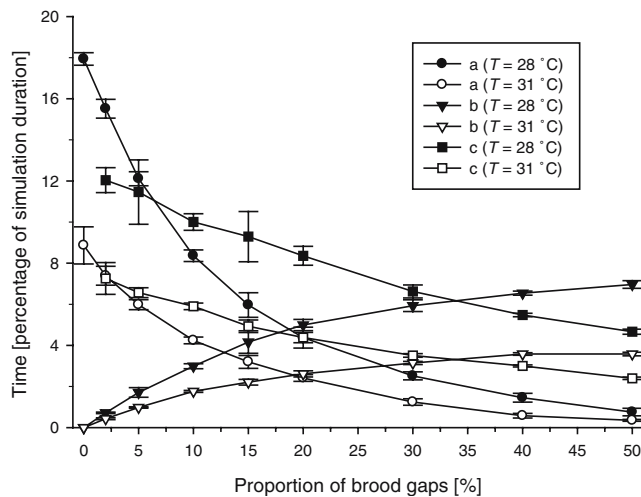


Fig. 2 Time spent on brood incubation **a** via the brood caps and **b** inside open cells (gaps) during the simulation (mean values and SD of five runs each; random distribution of gaps). Figures are expressed as percentage of the simulation time. Remaining time is spent on walking around without displaying specialised brood incubation behaviour and completes to 100% (not shown). The total time during which open cells are occupied by brood incubating cell visitors (**c**) is expressed as percentage of the maximum time (=number of gaps multiplied by 10 h simulation time) the agents might have spent inside these cells if all gaps had been occupied continuously during the whole simulation run. Symbols are connected by lines for better visualisation

are significant for n_{Gaps} from 2 to 20% (Mann–Whitney U tests, $N_1=5$, $N_2=5$, $U=0$, $P=0.0079$ in all cases) with one exception ($n_{\text{Gaps}}=2\%$, random distribution, $T=31^\circ\text{C}$: $U=3$, $P=0.0556$). At the optimum point, between 29 and 35% (random distribution) and 38 to 43% (regular pattern) of the incubation time per brood cell are saved. However, most of this reduction is achieved when n_{Gaps} is raised from 2 to 10% (Fig. 1a).

If gaps are present ($n_{\text{Gaps}}=5, 10, 20\%$) but not used for incubation, there is no benefit, and the average incubation time per brood cell increases by factors of up to 1.2 instead of being reduced.

The results of the energetic efficiency study are essentially similar to those of the time measurements. The shape of the curves (Fig. 1b) varies with the ratio of $f_{\text{Air_Cap}}$ to $f_{\text{Air_Cell}}$, i.e. with the proportion of heat that bees on the comb surface emit in other directions than towards the brood comb on which they stand. The higher the ratio of $f_{\text{Air_Cap}}$ to $f_{\text{Air_Cell}}$, the better it is if incubation is achieved by cell visitors rather than by bees on the comb surface. The optimum is at $n_{\text{Gaps}}=2$ to 10% ($f_{\text{Air_Cap}}=2$) and at 20 to 30% ($f_{\text{Air_Cap}}=7$), with significant reduction in comparison to the initial values at $n_{\text{Gaps}}=0\%$ (Mann–Whitney U Tests, $N_1=5$, $N_2=5$, $U=0$, $P=0.0079$ in all cases) except for simulations with $f_{\text{Air_Cap}}=2$ at $T=31^\circ\text{C}$ (random distribution: $U=6$, $P=0.22$; regular pattern: $U=8$, $P=0.42$).

Heating inside cells becomes less efficient if many gaps are present and the number of brood cells adjacent to a gap

decreases. Therefore, the different optimum proportions in Fig. 1 represent a balance between the advantages and disadvantages of both heating strategies under different conditions.

Discussion

The results of our study show for the first time that honeybee colonies benefit from the presence and usage of a small proportion of gaps in the sealed brood area. Although heat production inside gaps is not essential for the maintenance of optimum brood temperature, it clearly reduces the colony's costs (energy and time) per larva.

In comparison to sealed brood nests without any gaps, a small increase in n_{Gaps} has a strong influence on the spatial distribution of gaps and sealed cells relative to each other (Kleinhenz, unpublished data). Cell visitors may transfer heat to up to six surrounding brood cells if only few gaps are present, but only to five or less brood cells if n_{Gaps} increases and more gaps are next to each other. This reduces the advantage of heating inside cells and explains why small proportions of gaps are beneficial, whereas high proportions are not.

The energetic benefit (Fig. 1b) depends on the proportion of heat that bees lose to the air. In a three-dimensional hive, warming of the air between two combs may slow down the cooling of the brood, or it may warm an adjacent brood comb. Therefore, Fig. 1b applies best to the periphery of the hive where brood combs are adjacent to storage combs that do not need to be warmed, to observation hives with combs on top of each other and to thinly populated hives where trapping of warm air by the bees' interlacing thoracic hairs and by closing of ventilating passages (Southwick and Heldmaier 1987) is less efficient.

The term "optimum" point for certain values of n_{Gaps} refers to the shape of the curves and is not meant to imply that the bees work on the establishment of a certain number or a spatial pattern of gaps under different conditions. Occurrence and distribution of gaps are determined mainly by the queen's spatial and temporal egg laying pattern and by subsequent removal of brood. Although the brood nest develops in a somewhat orderly fashion, the queen's egg laying pattern is quite unsystematic with the queen often changing between comb sides and to different combs (Park 1946; Leuenberger 1974; Camazine 1991). This behaviour leaves gaps that are not perfectly filled during later visits to the same region. For example, half of the egg deposits observed by Camazine (1991) took place at distances of one to six intervening cells to the nearest brood cell. Additional gaps result from the early removal of brood of all stages (Fukuda and Sakagami 1968) for numerous reasons that may not be considered in detail here.

One factor that may account for up to 8% gaps even in genetically well-mixed (Holm 1997), healthy and well-nourished colonies is the removal of diploid drone larvae shortly after hatching from the egg (Woyke 1984; Santomauro et al. 2004). Gap proportions of 4 to 10% are common and considered to be harmless (Winston et al. 1981; Woyke 1984; Santomauro et al. 2004).

Even at these natural and low proportions of n_{Gaps} , there is a significant reduction in the colony's efforts, e.g. by 17 to 20% ($n_{\text{Gaps}}=5\%$) and by 25 to 32% ($n_{\text{Gaps}}=10\%$) of the incubation time per brood cell (Fig. 1a, $T=31^\circ\text{C}$).

In colonies with high rates of inbreeding, the removal of diploid drones leads to disastrous brood losses at rates of 25 to 50% above the common level (Woyke 1984). Such high values of n_{Gaps} should be avoided because they reduce the colony growth and indicate a poor condition of the colony. In addition, the regulation of brood nest temperature is also less economic and more difficult to achieve by demanding more energy and time per brood cell from the bees.

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