Analysing honeybees' division of labour in broodcare by a multi-agent model

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Abstract

We describe a multi-agent model of a honeybee colony and show several applications of the model that simulate experiments that have been performed with real honeybees. Our special emphasis was on the decentralized, self-organized regulation of brood nursing, which we successfully simulated: We found that brood manipulations, food-deprivation experiments and colony-size manipulations can be explained by the mechanisms we implemented into our model described here. Our agents can perform various tasks (foraging, storing, nursing). The model is spatially resolved, and contains a designated broodnest area as well as a designated honey/nectar storage area. All bees (and larvae) consume nectar/honey at a task-specific rate, allowing us to track the flow of nectar through the colony. Several kinds of stimuli, which are important for division of labour, were modelled in detail: dances, contact stimuli and chemical signals.

Introduction

The ability of social insects to divide the colony's work via specialisation, polyethism and task partitioning has fascinated scientists since decades. For example, early work of (Lindauer, 1952; Rösch, 1952; Sakagami, 1953) described the impressive ability of honeybees to specialize on different tasks based on an age-based scheme (temporal polyethism). In recent years, several conceptual models have been proposed to explain the basic proximate mechanisms that lead to division of labour in social insects in general, see Beshers and Fewell (2001) for a review, and for honeybees in detail: Age-based polyethism (Seeley, 1982; Johnson, 2005), regulation by queuing delays (Seeley, 1992), foraging for work theory (Franks and Tofts, 1994), threshold reinforcement (Theraulaz et al., 1998), and social inhibition (Beshers et al., 2001). Many of these concepts were also investigated by mathematical models and computer simulation (Anderson, 1998; Gautrais et al., 2002). One the one hand, these models focused very well on the specific key process that they were built to examine, on the other hand, they lack many specific details that are significantly affecting the behaviour of social insects. To fill this gap and to allow specific simulation of honeybees' division of labour, we constructed a multi-agent model of a honeybee colony that builds on the
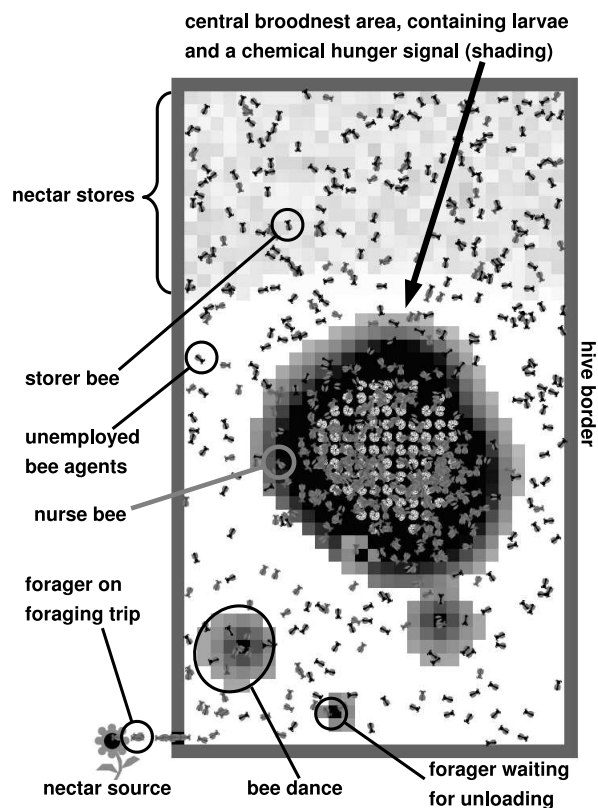

Figure 1: Typical screenshot of our multi-agent simulation at run-time. Bee agents move across the hive space and, depending on their history, emit several sorts of stimuli: waggle/tremble dances and offering signals. Hungry larvae also emit chemical hunger stimuli, which diffuse in the central broodnest area. Unemployed bees can react to all of these stimuli and switch to one of the modelled task cohorts.

ideas of the before mentioned models and incorporates several important honeybee specific details:

1. A typical spatial distribution of brood and food in the hive.

2. Complex behavioural programs of specialized workers.

3. Characteristics of the spreading of different kinds of stimuli (chemicals, sounds/vibration, light).

4. Agents physiology (energetic expenditures).

5. Flow of nutrients among the agents and the combs.

Our multi-agent model (named TaskSelSim) is implemented in NetLogo (Wilensky, 1999). The implementation of the model (equations, parameter values) have been described in detail in (Schmickl and Crailsheim, 2008b). In this article, we describe the models implementation in a lower degree of details and concentrate on those details that are important for the focal questions described here: How does the brood status affect the division of labour in the simulated honeybee colony and how does the colony status affect the brood nursing. Other aspects of division of labour (effects of selective removals/additions of task cohorts) were already investigated in (Schmickl and Crailsheim, 2008a), thus we did not perform such experiments in the study presented here.

Brood nursing (feeding brood with honey, pollen and pollen derived gland products) is a distributed process in a honeybee colony: Each specialised nurse bee feeds many larvae sequentially and each larva is fed by many nurses. The brood is allocated in a central area in the hive, one larva is occupying one comb cell. We studied the nursing of brood in honeybees with several ethological studies, see Schmickl and Crailsheim (2002). These experiments showed that brood nursing is regulated in a homoeostatic, adaptive way. It was shown by (Huang and Otis, 1991b) that nurse bees preferentially inspect comb cells that are occupied by larvae and that artificially starved larvae receive preferential nursing (Huang and Otis, 1991a). The hunger state of a larva is communicated to nurse bees by emission of chemical substances (pheromones). All of these facts were incorporated in our model (together with an implementation of the foraging process and the nectar storing process), to generate a model that is able to integrate many (separately derived) hypothesises of honeybees' regulation of division of labour into one single consistent process.

The Model

Our model depicts one honeybee colony consisting of agents (adult bees, larvae), stimuli (dances, contact stimuli, chemical signals, light) and resource stores (nectar and honey is used synonymously). The hive space is modelled in discrete patches (31 x 52) but the adult bee agents can move across these patches in continuous motion. The intensity of local stimuli is modelled discrete, following the grid of patches that represent the comb cells. Figure 1 depicts the typical spatial distribution of agents, stimuli and resource stores.

Within each time step, the following functions are executed iteratively:

1. All patches update their status (decay of chemicals).

2. All agents emit stimuli, chemicals are diffused.

3. All agents consume nectar.

4. All adult agents decide to engage or to give up a task.

5. All adult agents perform behaviour according to their task.

Modelled Tasks

Depending on the task the bees are engaged in, they perform the following behavioural programs:

Unemployed bees: These bees move randomly in the hive. In our model, bees had to switch to this unemployed state at least for one time step before they could engage in a different task.

Forager bees: These bees leave the hive with a low (but sufficient) crop load. They fly to the nectar source, fill up their crop and fly back to the entrance. There they emit the unloading stimulus to attract nearby storage bees which take over the nectar load. After some time of random movement in the hive, they can perform a waggle or a tremble dance (see below for more details). Afterwards, they leave the hive again towards the nectar source.

Storer bees: These bees wait near the entrance for returning foragers. They take the crop load of returning foragers and head towards the storage area (see Figure 1). They drop their nectar load there and head back towards the entrance.

Nurse bees: These bees navigate (uphill) in the chemical stimulus emitted by hungry larvae. If they are located on a patch containing a hungry larva, they start to feed this larva until it is saturated or the nurse is almost empty. These feedings last for several time steps.

Larvae: The brood resides in cells (patches) in the central broodnest area (see figure 1). Larvae cannot move. If they have low nectar reserves, they emit a chemical hunger signal. See below for more details.

Modelling the Stimuli

In our model it is important that stimuli differ significantly in their dynamics and in their range: Contact stimuli are emitted by returning forager bees to attract storer bees to take over the nectar load. These signals have a short range ($r = 1$) only and stop immediately after the forager is entirely unloaded. Depending on the waiting period a forager searched for a storer bee, it then performs either a 'waggle dance' ($T_{search} <= 20$) to recruit more forager bees or a 'tremble dance' ($T_{search} >= 50$) to recruit more storer
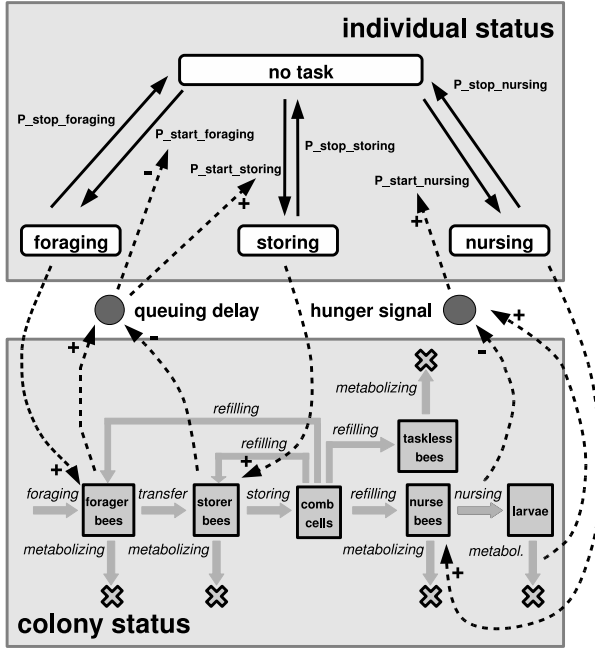
Figure 2: The flow of nectar, bees' metabolism and task selection of our agents. Top: Individual task selection depicted as a state automaton. Middle: Most important regulation feedbacks. Bottom: Task cohorts as compartments in the flow of nectar in the colony. Rounded boxes represent individual tasks. Solid arrows indicate task switches. Dashed arrows indicate dependencies ('A is affecting B'). Rectangular boxes represent worker cohorts, larvae or combs. Solid arrows indicate nectar flows. The flower represents a nectar source, the cross-like symbols represent sinks.

bees. Both stimuli spread wider ($r = 3$) and decay non-linearly ($\frac{1}{d}$) with increasing distance from the emitting bee. As soon as the dancing bee stops, the emitted dance signal disappears also from all other patches immediately. In contrast to that, the chemical stimuli emitted by larvae stay much longer and spread wider: They diffuse to all nearby patches and decay slowly:

$$\frac{\partial C(\mathbf{x})}{\partial t} = D\nabla^2 C(\mathbf{x}) - \mu C(\mathbf{x}) + \alpha_i(t)L_{hungry}(\mathbf{x}), \quad (1)$$

where $C(\mathbf{x})$ is the local concentration of hunger pheromone at position $\mathbf{x}$, μ is the rate of pheromone decay, α is the addition rate of pheromone produced by a hungry larva. $L_{hungry}(\mathbf{x})$ is set to 1 in case that there is a hungry larva at position $\mathbf{x}$, else it is set to 0.

In case that the larva at position $\mathbf{x}$ has a nectar reserve below the hunger threshold $cr_{low} = 0.25$, alpha scales linear from 1 down to 0, as described in equation 2.

$$\alpha_i(t) = 1 - \frac{v_i(t)}{cr_{low} \cdot capacity_{larva}} \quad (2)$$

If the larva has more nectar in its reserves, then the value of $\alpha_i(t)$ is set to 0. A hungry larva at position $\mathbf{x}$ is referred as larva i. The nectar reserve of this larva is described as $v_i(t)$, the maximum storing capacity of a larva was set to $capacity_{larva} = 0.33$. The 'diffusion term' was implemented numerically (and discrete): we used the build-in function "diffuse" available in the NetLogo programming environment. The light stimulus decreases linearly with increasing distance from the hive's entrance and is used for navigation of foragers for leaving the hive and for navigation of storer bees for approaching the entrance area and for approaching the honey area. Nurse bees navigate uphill in the chemical pheromone field to find hungry larvae to feed and move towards darker areas to find honey cells for refills.

Simulated physiology

An adult bee can hold a maximum of 1 unit of crop load. A larva can hold 0.33 units at maximum. Adult bees consume their nectar loads at a low rate of $cr_{low} = 0.0004\ units/step$, flying foragers consume at a higher rate $cr_{high} = 0.001\ units/step$. Larvae consume nectar at the rate $cr_{larva} = 0.0004\ units/step$. If an agent (bee or larva) runs out of nectar, it dies and is removed from the system. The bottom of figure 2 shows these consumption flows.

Modelling Division of Labour

The most important aspect in our model is the implementation of the task selection mechanism. We followed the approaches of Gautrais et al. (2002) and implemented a threshold based system. Each type of local stimulus can motivate an unemployed adult bee agent (task = 'no-task') to join one of the tasks $m \in \{$ 'foraging', 'storing', 'nursing' $\}$. See figure 2 (upper part) for the possible task transitions. Whenever one of these stimuli exceeds an individual threshold of an agent i located on that patch x, the agent engages in the associated task m. Each of these thresholds is modelled in a non-linear manner, as is shown by equation 3. $p_{i,m}$ models the likelihood to engage in task m in one time step. $s_{x,m}$ is the local intensity of the task-associated stimulus. $\Theta_{i,m}$ is used to shift the threshold individually up and down, n is used to express the degree of non-linearity in these behavioural decisions.

$$p_{i,m} = \frac{s_{x,m}^n}{s_{x,m}^n + \Theta_{i,m}^n} \quad (3)$$

Employed bees switch back to the unemployed state with probabilities of $\lambda\prime_{nursing\prime} = \lambda\prime_{storing\prime} = 0.005/step$ and $\lambda\prime_{foraging\prime} = 0.001/step$. To allow specialisation within this system, the levels of the thresholds are adapted individually during run time. In the case that an unemployed agent engages in task $m\prime$, the $\Theta_{i,m}$ is reduced by ξ_m, making it

more likely that the agent will engage in this task in future. Whenever an unemployed agent does not engage in a task, the corresponding threshold is increased by φ_m, making it more unlikely that these behaviours will be triggered later on. In our simulations, all values of ξ were set to $\xi = 0.1$ and all values of φ were set to $\varphi = 0.001$. It was shown in (Schmickl and Crailsheim, 2008b) that these parameter values lead to plausible division of labour. In our simulations we used $n = 2$ for all agents and all agents initially started with Θ values of 0.001 for all tasks. During run time, values of Θ were confined between 0 and 1.

Initial Conditions

Our simulations were conducted with 700 adult bee agents and 100 larvae. The larvae were distributed randomly (normal distribution) around the center of the hive. All adult agents started in randomized positions and with randomized headings. Their initial task was set to 'no-task'. All agents had (uniformly) randomized crop loads.

Results

This article focuses on the aspects associated with the regulation of brood nursing, thus we manipulated the ratio of adult bees to larvae in our simulation experiments described here. We first simulated 10000 time steps of an undisturbed colony, to allow the colony to reach equilibrium in brood supply and in division of labour. At time step 10000, the whole simulation state was saved on hard disk. Starting with this saved configurations several perturbations were performed (addition of brood, removal of adult workers) and the resulting changes in task cohorts were measured. In these experiments, all adult bees started with Θ values of 0.
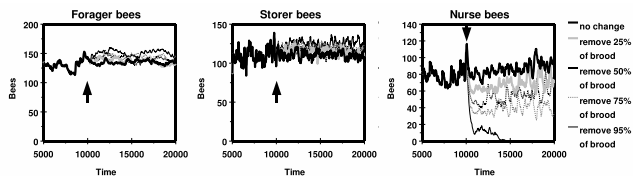
Perturbations of the adult-to-brood ratio

Figure 3: Removal of brood affects the size of the nursing cohort strongly. The additional workforce that gets available from abandoning brood care affects also the size of the other working cohorts. The arrows indicate the timing of the perturbation. Graphs show mean values (N=6).

The more brood was removed at time step 10000, the less bees performed the nursing task. This high abandonment from nursing made more bees available for the tasks of storing and for the foraging task, as can be seen in figure 3.
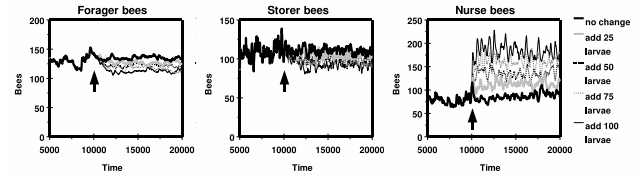

Figure 4: Addition of brood affects the size of the nursing cohort strongly. This binds additional workforce to the task of nursing, what in turn affects also the size of the foraging cohort and of the storing cohort. The arrows indicate the timing of the perturbation. Graphs show mean values (N=6).

Analogously we observed a significant increase of the size of the nursing cohort as we spontaneously added brood to the colony at time step 10000. This reduced the number of unemployed bees, in turn affecting also the task equilibrium of foraging bees and of storing bees, as shown in figure 4.
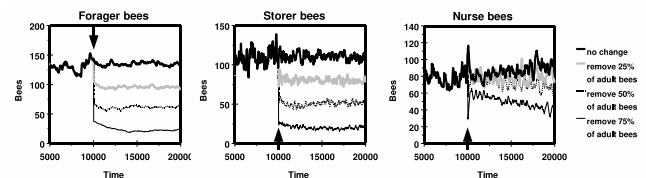

Figure 5: Removal of worker bees affected all task cohorts. The cohort of nurses bees was strongly affected only with the more extreme removal of worker bees. The arrows indicate the timing of the perturbation. Graphs show mean values (N=6).

As figure 5 shows, the removal of adult bees strongly affected all three task cohorts. The removal was a random pick across all task cohorts. While the cohorts of foragers and storers were affected significantly by all worker losses, the cohort of nurse bees was affected significantly only by the bigger losses of worker bees.

Nectar economics

During the experiments shown in the figures 3, 4, and 5, the colony structure was significantly altered at time step $t = 10000$. Since we also modelled the flow of nectar (nectar income and consumption), we could also investigate how these alteration affected the colony's nectar economics. Figure 6 shows these results: The removal of brood strongly enhanced the colony's net nectar gain, as a significant sink for nectar was decreased. In contrast to that, the addition of brood increased this important nectar sink, what had a detrimental effect on the colony's nectar economics. This effect was also observed by leaving the sink unchanged but

by decreasing the foraging workforce, as it happened by the removal of adult bees.
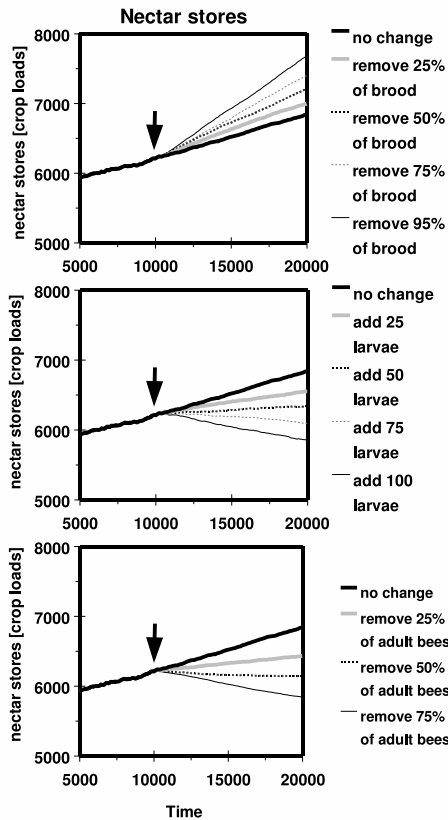

Figure 6: Removal of brood leads to strong increases of the colony's net nectar gain over time. Addition of brood or removal of workers lead to strong decreases of the colony's net nectar gain. The arrows show the timw of the perturbation. All graphs show mean values (N=6).

Scaling properties of division of labour

As shown above, colony manipulations affected the task cohorts and the colony's net nectar gain. As figure 7 shows, forager and storer cohorts are severely affected (high steepness of the regression curve) by removal of worker bees. Nurses and net nectar gain is affected by both, brood manipulation and by adult removal. Almost all correlations between perturbation strength and resulting cohort sizes were found to be linear. It has to be mentioned that the steepness of regressions varied significantly, what points towards different sensitivities of cohorts to perturbation types.

Nursing on the individual level

Empirical studies showed that nursing of brood is regulated in a supply-demand driven process. Huang and Otis (1991a) performed an interesting study, where they prevented a set
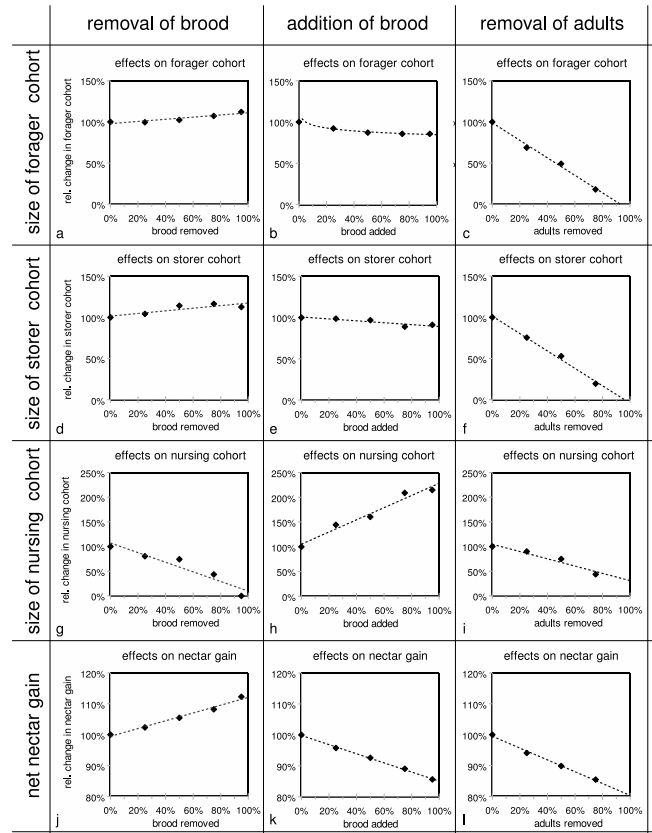

Figure 7: The effects of all perturbations scaled in most cases linearly with the strengths of the perturbations. The figures indicate the relative difference of the end result of the simulations ($t = 20000$) compared to the undisturbed control simulations. Graphs show mean values (N=6).

of 4-day old larvae from being fed by nurse bees with a cage that was placed around the larvae. They found that these starved larvae were fed preferentially by nurse bees after the cage was removed. We were interested whether or not such effects could be observed also in our model. Thus we (virtually) put a cage around a central spot in the center of the broodnest, what prevented the bees from entering this area. After 400 time steps with the cage preventing feedings, a fraction of the larvae died (see figure 8). The remaining larvae were fed preferentially during the first 1000 time steps after the cage was removed (figure 9). Later on, the formerly starved larvae were fed on average on the same level, but the mode of nursing was still altered due to experimental manipulation: Feedings were performed in a more oscillating manner, suggesting that disturbances of brood nursing could cause long-term alterations in the colonies nursing behaviour. Table 1 sums up the mean number of feedings per time-slot (which was 100 time steps wide) per larva for both

zones (central cage area, peripheral 'no-cage' area):

Phase (time steps)	Central area (cage)	Peripheral area (no-cage)
Pre (0 - 1500)	0.24 ± 0.16	0.24 ± 0.13
Experiment (1501 - 1900)	0 ± 0	0.24 ± 0.14
Post (1901 - 2900)	0.37 ± 0.64	0.22 ± 0.11
End (2901 - 5000)	0.24 ± 0.34	0.23 ± 0.08

Table 1: Statistical comparison of all 4 phases in both experimental zones. Means values were gained from all larvae in the corresponding zone per 100 time steps. $\pm$ indicates the corresponding standard deviations in these datasets.

(a) t = 20 steps (b) t = 300 steps

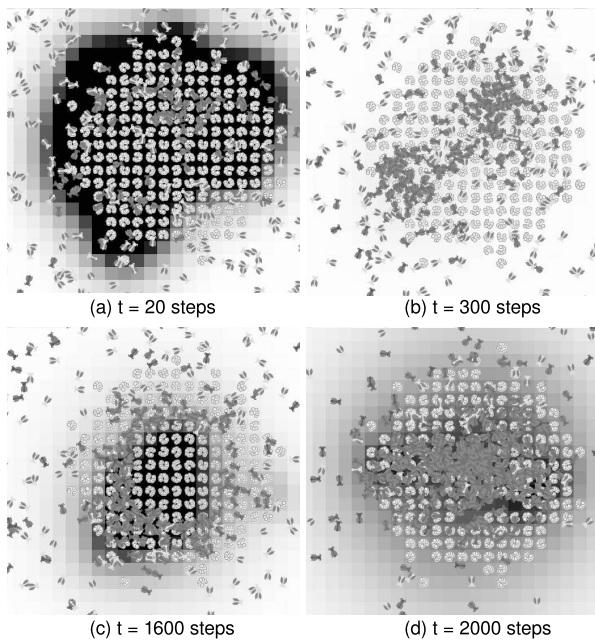(c) t = 1600 steps (d) t = 2000 steps

Figure 8: (A) Initially the brood starts hungry and emits a lot of hunger signals. (B) After 300 time steps, the nurses satisfied the brood and kept it on a rather fed status. (C) At time step $t = 1500$, the (virtual) cage was installed around the central brood nest area. At $t = 1600$, many hungry larvae can be found in the center, emitting strong hunger stimuli. (D) After removal of the cage at $t = 1900$, the central brood is either dead (removed) or very hungry. At $t = 2000$, nurses aggregate in this area and feed frequently.

Specialization in the nursing task

In additional simulation runs, the development of thresholds in big and small colonies with low and high brood state was observed. In these experiments, all Θ values were initially
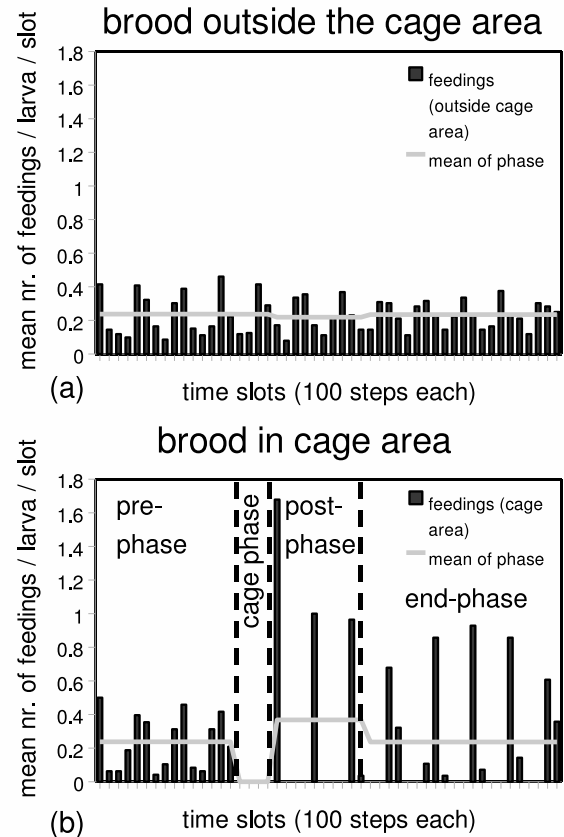

Figure 9: (A) In the area outside the cage-zone, larvae are fed in all experimental periods on the same average rate. (B) In the pre-experimental period, central and peripheral larvae are fed on the same level. During the cage-period, no feedings can occur. During the first 1000 time steps after the cage's removal, the remaining starved larvae are fed preferentially. Also the oscillations increased significantly. In the final period, the level of feedings returns to the initial value, but the rhythmicity stays on an increased level.

randomized uniformly between 0 and 1. After 10000 time steps, the values of $\Theta_{nursing}$ were measured. To speed up the specialization process, all ξ_m values were increased to 0.2 in these experiments.

The first simulation we performed was with the colony status we used also in the simulations described in the previous sections (700 adults, 100 larvae). As can be seen in figure 10, approx. 10% of the bees developed into highly specialized nurses. The majority of bees developed into highly specialized storage bees or into 'partly-specialized' storage bees. Although we observed between 65 and 120 forager bees throughout the run-time of the simulation, the observed degree of specialization for this task was not comparable to

the degree of specialization of the other tasks. In (Gautrais et al., 2002) it is predicted by another model, that the degree of specialization increases with colony size. To investigate this question also with our model, we scaled down the colony size (adults and brood) by the factor $\frac{1}{4}$. Please note that the nursing workload per bee was kept constant. As can be seen in figure 11, the degree of specialization decreased, especially with the nursing task and with the storing task.
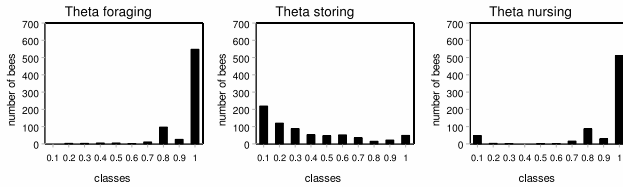
Figure 10: Degree of specialization to our modelled tasks in a simulated colony consisting of 700 adult bees and 100 larvae. Low theta values ($\Theta <= 0.2$) are interpreted as 'high degree' of specialization. Values of $0.2 < \Theta < 0.8$ are interpreted as partially specialized bees. Higher values of Θ are interpreted as bees not specialized to the specific task.
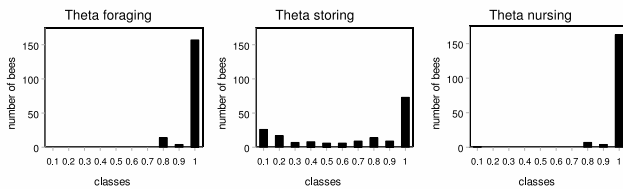
Figure 11: Degree of specialization to our modelled tasks in a simulated colony consisting of 175 adult bees and 25 larvae. Low theta values ($\Theta <= 0.2$) are interpreted as 'high degree' of specialization. Values of $0.2 < \Theta < 0.8$ are interpreted as partially specialized bees. Higher values of Θ are interpreted as bees not specialized to the specific task.

In a final simulation experiment, we doubled the work load per adult bee compared to the settings shown in figure 10. As can be seen in figure 12, this increased preferentially the degree of specialization of nurse bees, as the number of highly-specialized nurses more than doubled.

Discussion

We showed that a threshold-based model can suffice to simulate honeybee-specific division of labour. By performing and analyzing our simulations, we learned that having a reactive system of task cohorts, which is able to react plausibly to perturbations of colony structure, is not a guarantee
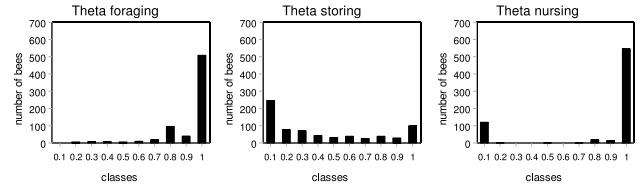
Figure 12: Degree of specialization to our modelled tasks in a simulated colony consisting of 700 adult bees and 200 larvae. Low theta values ($\Theta <= 0.2$) are interpreted as 'high degree' of specialization. Values of $0.2 < \Theta < 0.8$ are interpreted as partially specialized bees. Higher values of Θ are interpreted as bees not specialized to the specific task.

for having task specialisation and de-specialization of workers: As our figures 3, 4, 5 and 6 show, our modelled colony reacts very plausibly to the induced perturbations. When we investigated whether or not the nursing received by individual larvae after a deprivation experiment is predicted plausibly by our multi-agent simulation, we found that the nursing regulation reflects empiric results very well.

Although we found division of labour and specialization of hive-bees (nurses, storers), figure 10 tells us, that the foraging cohort did not show the expected high degree of specialisation in our simulations. The threshold-response system was able to model specialisation of nurses by chemical brood stimuli at a very high degree. We found also many bees highly specialized to the task of storing. But also a high number of 'semi-specialized' storers ($0.2 < \Theta < 0.8$) was found. Most foragers showed only a low degree of specialization, indicating that foragers are not often re-recruited to the foraging task after they abandoned from foraging. We had between 65 and 120 foraging bees present at all times, but almost all foraging bees performed just one or two consecutive engagements, having several round-trips. The fact that we still observed task cohorts that reacted adaptively to perturbations can be reasoned by the equilibria that emerge: Foraging has a high turn-over number, that means foragers that quit the task once in our model are not often re-recruited. But simultaneously many other bees, that performed other tasks before, are recruited to the task of foraging. Obviously, this suffices to allow an adaptive equilibrium-based division of labour.

We conclude that threshold reinforcement (Theraulaz et al., 1998; Gautrais et al., 2002) is well suited to produce plausible specialization in tasks that are associated with very durable, time-persistent and spreading stimuli, like the pheromones that stimulate nursing behavior. Also the storing task has a high density of stimuli (tremble dances, every returning forager emits the 'storing' stimulus), but foraging is induced only by the (relatively rare) waggle dances.

As these dances do not occur at a comparably high frequency (only some foragers perform a waggle dance), re-recruitment is hard to explain by just this stimuli alone. In nature, foragers are a well specialized group in the honeybee society, thus we can assume that we will have to incorporate other additional factors to achieve the observed high specialisation of forager bees: shaking signals, stop signals and a (probably age-related) higher predisposition for the foraging task, as it can be easily implemented into our model by a slight downward-bias of $\Theta_{foraging}$ in a specific group of bees which represent 'older' bees. In addition, motivation for foraging can be also influenced by physiological properties of the bees, which reflect often characteristic hive conditions, as was demonstrated in (Camazine, 1993). We conclude that, incorporating additional regulatory systems and motivational aspects of bees, as for example temporal polyethism (Seeley, 1982; Johnson, 2005) can significantly improve the models predictions concerning foraging specialization.

For interpreting the observed differences in task specialization, we had to consider also the regions of the hive in which the recruited workers tend to stay. These regions include a specific mixture of stimuli, thus determining also the likelihoods to switch to other tasks. Such effects are discussed in the 'foraging-for-work'-theory, as it is described in (Franks and Tofts, 1994). By working with and on our model we learned that honeybee-specific division of labour cannot be modelled with the threshold-reinforcement model alone. We developed the idea that several of the discussed concepts of honeybees' division of labour have to be implemented into one single model, which then represents an integrative approach to understand honeybee's' division of labour. By extending our model in these directions, we will pursue this scientific goal.

Acknowledgements

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