

Task Selection in Honeybees - Experiments Using Multi-Agent Simulation

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One of the most interesting questions about social insects is how task allocation is controlled. Often specialization of individual animals occurs; there exist different hypotheses to explain this phenomenon. By using multi-agent simulation we want to gain evidence for the hypothesis that in honeybees (*Apis mellifera*) the fitness of a colony increases with increased variation of individual response thresholds, which would result in specialization. Based on a rather complete model of activities performed in a bee hive we conducted simulation experiments using different kinds of variation in task selection parameters. According to global measures of colony performance we showed that merely by variation of individual dispositions to engage in certain tasks the effectiveness of the hive increases.

1 Motivation

Honeybees (*Apis mellifera*) are considered to be one of the most highly developed social insects exhibiting very well adapted collective behaviors. The examination of the mechanisms that lead to these emergent patterns can be fruitful for many reasons. There is a wide potential for new optimization methods derived from models of bee behavior, analogous to the „Ant Optimization“ developed from models of pheromone recruiting that can be found in ants [1]. On the other hand many mechanisms are not yet fully understood from a biological point of view. Thus modeling the behavior and interactions of individual bees in a hive and observing the emerging global pattern can still lead to a deeper understanding and give new incentives for further practical research.

An outstanding example for an important mechanism, the origins of which are not completely settled, is how specialization emerges by differential task selection (for a review see [2]). Although every bee is - from a physiological point of view - able to carry out every task coming up in a hive, there seems to be specialization among the individual bees. The reasons for this are being debated. On the one hand there is a change in the tasks selected by worker bees as they age. Franks and Tofts propose in [3] a stimulus-controlled mechanism, the foraging-for-work hypothesis: A young, recently hatched bee encounters itself among eggs, larvae and pupae. Thus the first tasks it perceives are the ones related to brood care. Becoming elder it starts to leave the brood area and thus discovers other tasks. Other models of the mechanisms that lead to specialization include internal factors that change with age, for example hormone titers (as in [4]). On the other hand bees seem to have individual predisposition to prefer certain tasks. This may be due to genetic determination. The queen is often fertilized by more than 10 different drones; this leads to a greater genetic variation among the individual bees of one hive than simple recombination alone. Thus there are bees that react to some stimuli faster than others [2], and specialization could originate from these differences. The ultimate cause for this behavior and the specialization of individual bees could be an increased efficiency of specialized bees compared to „generalists“. However, this increased efficiency has not been shown. We want to examine if there could be advantages in this kind of variation for the bee colony as a whole without increased efficiency of individual specialized bees.

We compare task selection mechanisms with and without individually varying sensitivity thresholds in combination with an age-bound mechanism, thus realizing a model that incorporates genetic as well as age- and environment-linked endocrine factors in task selection [5]. As a basis for simulation experiments we use a behavioral model of individual bees that incorporates many different tasks that can be found in a hive. These behaviors and their results are highly dependent on each other and part of many feedback loops (described in [6]). Thus there are effects that are important for the validation of the model that can not be observed when focusing on single phenomena [2].

After describing the simulation environment we used for our experiments, the base model of honeybee behavior is introduced. In section 4 the experiments and results are presented. The paper ends with a conclusion and an outlook on further work.

2 Multi-Agent Simulation

For modeling and simulation of societies like colonies of social insects many different approaches are possible: On one side the complete group can be seen as one system and one can model the variation of its parameter on the macro level. This paradigm yields several disadvantages. The most important ones are that no variations in the behavior of the individual can be considered and that differences in the spatial structure of the entities' environment cannot influence their behavior [7]. Other forms of modeling societies generate the collective behavior from „bottom up“. Different mathematical micro-simulation approaches result in large equation systems, e.g. modeling via decision matrices or stochastic processes, thus individual or spatial variations can hardly be incorporated, see e.g. [8] or [9]. On the other hand modeling societies based on cellular automata or multi-agent systems enables the researcher to specify the local behavior of the individual spatial unit or entity. The behavior of the complete system is directly reproduced by simulating the actions of the individuals. As our research focus lies on the behavior and interaction of individual entities and not on special spatial pattern (like for example in [10]), we decided to use multi-agent simulation.

Multi-agent simulation is not a new technique for simulating insect societies. More than 10 years ago Deneubourg et al. modeled foraging and path recruiting behavior of ants based on very simple rules [11], [12]. They also

reproduced building behaviors. Simple agents react only to the environmental shapes they perceive and thus are able to construct complex nest structures without a priori map [13], [14]. Besides this work that focuses on single, rather restricted phenomena there is only little effort regarding more complete insect models that are required for task allocation simulation. [15] combines dominance interaction between individual agents influencing their „force“ with interaction between the agents and their environment that triggers and reinforces activities, either brood-tending or foraging. As the „force“ of a modeled wasp determines its general activity and moving speed and thus their interactions, a task specialization can be observed in the modeled colony.

As a basis for modeling and simulating honey bee behavior we used SeSAm (**Shell for Simulated Agent Systems**) [16], an improved version of the AL-OSIS system, that was specially developed for modeling ant behavior [17]. This simulation shell provides a generic environment for modeling and experimenting with agent-based systems with a special focus on supporting the construction of complex models. Because a graphical interface for implementing a model, built-in animation capabilities, tools for collecting and analyzing protocol data, etc. are provided, even scientists without traditional programming experience are able to build and experiment with multi-agent models.

In SeSAm the simulation of the environment is based on two-dimensional gridmaps. A third dimension can be represented as a combination of several two-dimensional maps. Every grid can carry a special amount of information (e.g. chemical trails) or objects. The latter may be resources or agents. Agents execute actions whereas resources are not allowed to actively influence the world. To enrich the environment, it is possible to define events as changes in the environment without a specific source. During a simulation experiment these events may happen at certain intervals, with a certain probability or in a specific situation.

An agent is specified by fixing four categories: 1. Sensoric abilities, 2. internal parameters, 3. the action selection procedure including all internal representation used for it and 4. the effectoric abilities (changing internal and external world). The SeSAm system provides default solutions for each of these categories. The standard primitive sensoric and effectoric abilities can be adapted domain-specifically using graphical editors. Every agent has a current activity that determines the actions it executes on itself and on its environment once every time step. This activity can be selected in two ways: Either because it is contained in a skeletal plan that the agent has chosen to pur-

sue or because it is selected as a reflex by applying a rule with a higher priority. The termination of the current activity may be driven by specified goal situations or simple time-outs. Reflex rules specifying emergency situations can interrupt the normal execution at any time. In order to support modeling we introduced behavioral roles to structure the set of activities, skeletal plans and emergency rules. These roles correspond to stereotypes. In contrast to the agent class that e.g. represents the modeled species, agents can switch their role.

This structured agent architecture provides the possibility to build large behavioral models remaining easily accessible and transparent not only to the developer herself.

3 A General Model of Bee Behavior

Our simulation was intended to model all important aspects of a bee's life inside the hive. This includes individual development from egg to adult and adults performing tasks such as queen and brood tending, storing, retrieving and distributing honey and pollen as well as communication and foraging. Which task a bee performs at one point in time is dependent on the bee's behavioral role (see below), the cues it perceives in its environment, and its response thresholds to those cues. Thus every bee reacts only on local cues and its internal state.

„Behavioral roles“ are intended to model physiological differences between bees. Reflecting the fact that in honey bees some tasks require the development of certain glands (e.g. the hypopharyngeal gland for brood feeding) that change their function during a bee's life, each bee is assigned a certain „behavioral role“. Bees switch these roles when they age, depending on signals received (such as the shaking signal or tremble dance performed by forager bees), on internal predisposition and on the amount of time they need to find a task, which is a measure of how needed the completion of this particular task is at the moment. This mechanism is similar to the one described in [4]. The bees have an internal parameter, which can be seen as analogous to

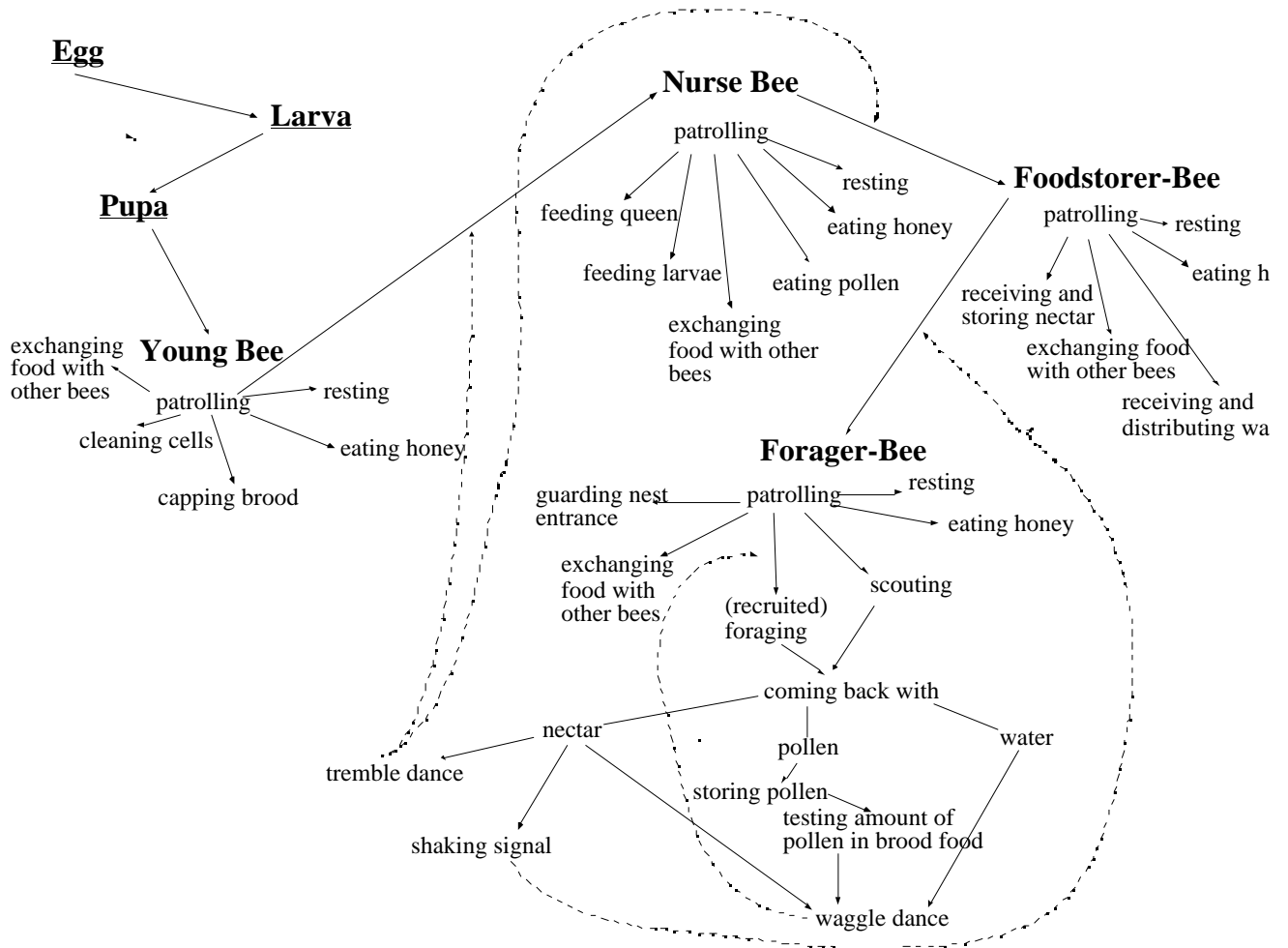


Figure 1: Simplified schematic representation of behavioral roles and activities that can be performed by the modeled bees; bees go through all behavioral roles, from egg to forager bee, in their life (along thick arrows), but the time they stay in a certain role can differ. When selecting a new activity, bees follow the thin arrows; when they finish a task, they generally return to the ‘patrolling’ activity before choosing a new task.

the juvenile hormone titer, which determines which tasks they are able to perform. This parameter increases as bees age, but the increase depends also on signals and cues received.

Bees in any „role“ can engage in a number of activities. The selection of the next activity depends on external stimuli and a „threshold“ for this special activity. Generally the probability with which a bee engages in a certain task is proportional to the distance of the stimulus, e.g. the larva that has to be fed, and to the reciprocal value of its threshold for that activity. These thresholds can thus be used to model differences in genetic predisposition of individual bees to do certain tasks.

A schematic representation of the tasks and roles in the model is given in figure 1. The activities in the different behavioral roles can be seen, as well as the feedback loops which influence the time at which workers switch roles and which thereby regulate the amount of workers allocated to these roles (dotted arrows). The sequence of roles is as follows: A bee starts its life when an egg is laid by the queen. If it is fed enough, it then develops into a larva, pupates, and finally hatches as an adult ‘young bee’. Young bees and ‘nurse bees’ (who care for brood and feed the queen) mainly engage in tasks in the brood area, while other adult bees (food-storers and foragers) often stay near the nest exit. This sequence of behavioral roles has been described by [6] and [18].

All activities taking place inside the hive are modeled explicitly, i.e. the bees move around in the hive while engaged in their tasks. The foraging of bees however, taking place outside the hive, is only modeled insofar as bees leave the hive and return with a load of honey, pollen or water. The time this takes and the amount brought back depend on whether the bee was scouting (then both values are chosen randomly) or was a recruited forager, in which case values are determined by the information given to the bee during the recruitment (waggle dance)

4 Experiments in Task Selection

The aim of this study was to examine the consequences of variability in the individual bees’ dispositions to do certain tasks. We wanted to see if variation *per se*, without increased efficiency connected to it, would have an effect on the overall performance of the bee colony. This variation can be understood as genetic variation, for example due to multiple matings of the queen, or as

specialization of individuals on certain tasks over longer timespans. We modeled this variability in dispositions as variation in the response „thresholds“ (see model description).

Three types of variation in these thresholds were introduced:

1. uniform - all bees have the same value (5) for all thresholds (all activities), thus each bee has the same disposition to engage in each task
2. random (small interval) - each threshold is randomly determined at the beginning of a bee's life and has a value between 3 and 7 (included)
3. random (large interval) - same as 2., thresholds can have values between 1 and 9

10 simulation runs were carried out for each of these variation types.

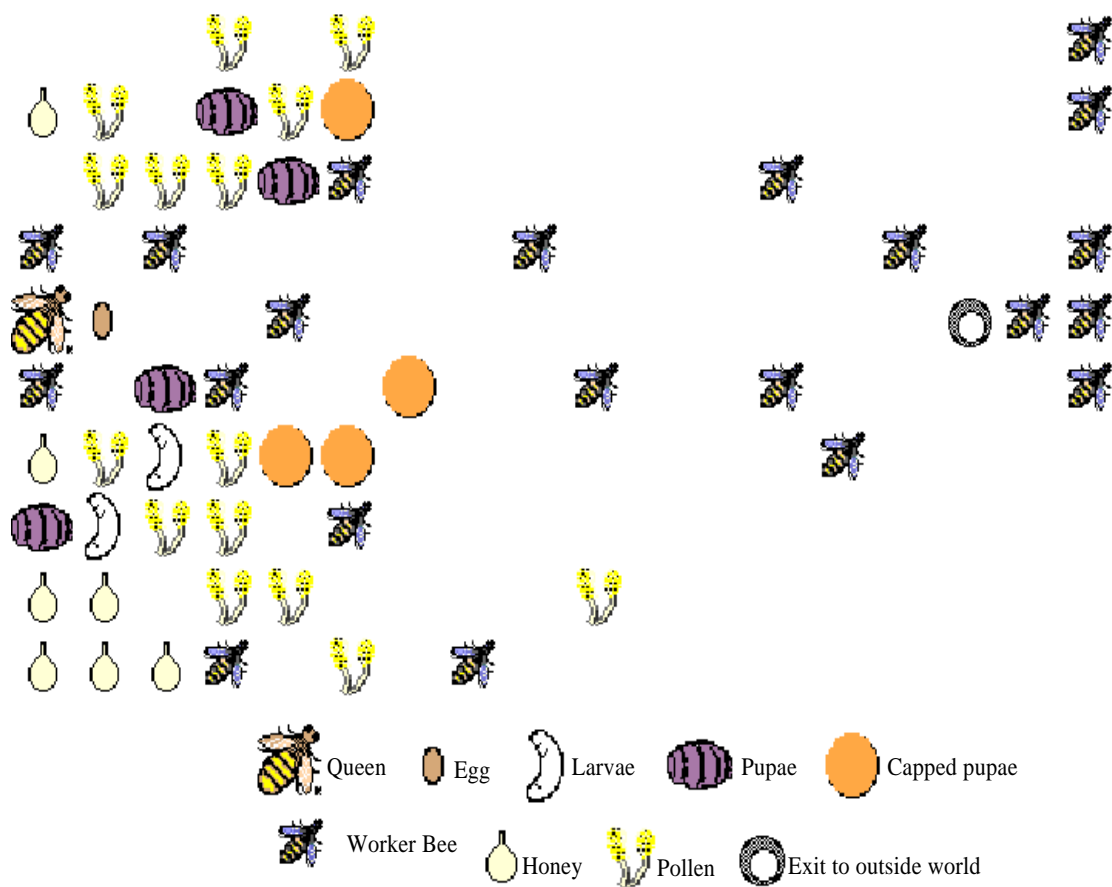


Figure 2: Snapshot of the situation inside the hive during an animated simulation experiment, showing the positions of agents (bees) and objects on the comb at this point in time

As measure of the colony's performance we used two parameters. One is the number of eggs laid by the queen, which depends on how much the

queen is fed; the other is the number of larvae that pupate, which depends both on the number of eggs laid and whether the larvae are fed enough at regular intervals over a period of time. The experiments were run over a period corresponding to 12 days, the elementary time unit of the simulation being one minute.

In each experiment we started with a very small hive of 12x18 cells containing a queen, eggs, larvae, pupae, several adults and some honey and pollen. The bees started in different behavioral roles and their ages were evenly distributed over the lifespan. A graphical representation of a situation during one of the runs can be seen in figure 2.

5 Results

The results of the simulation experiments are given in table 1. The parameters correlating with the fitness of the hive, number of eggs laid (varying between 4 and 54) and the number of larvae that pupated (varying between 0 and 12), were smallest in the experiments with uniform thresholds and largest in experiments with thresholds varying between 1 and 9. Figures 3 and 4 show a comparison of the development of these two parameters over the course of the experiments.

Table 1: Results of simulation experiments - * indicate significant difference from experiment 1 (Mann-Whitney-U-Test)

Average of 10 runs +/- standard deviation	Experiment 1: uniform thresholds	Experiment 2: random thresholds (small interval)	Experiment 3: random thresholds (large interval)
of eggs laid	16.3 +/- 9.3	26.9 +/- 6.5 *	29 +/- 14.5 *
of larvae pupating	2.7 +/- 3.1	5.0 +/- 1.7 *	4.2 +/- 3.8

In all cases most or all of the bees in the hive had died by the end of the simulation run. The reason for this is maybe that not all parameters in our model had realistic values, and probably also that the colony was simply too

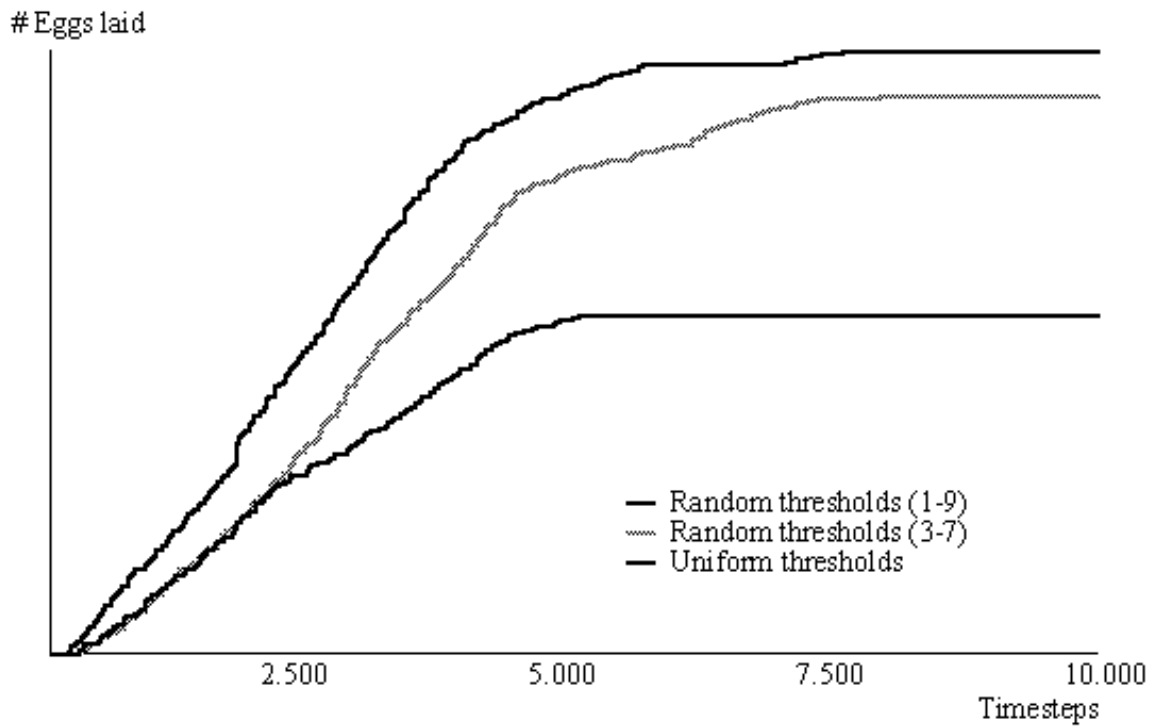


Figure 3: Average number of eggs laid in 10 simulation runs.

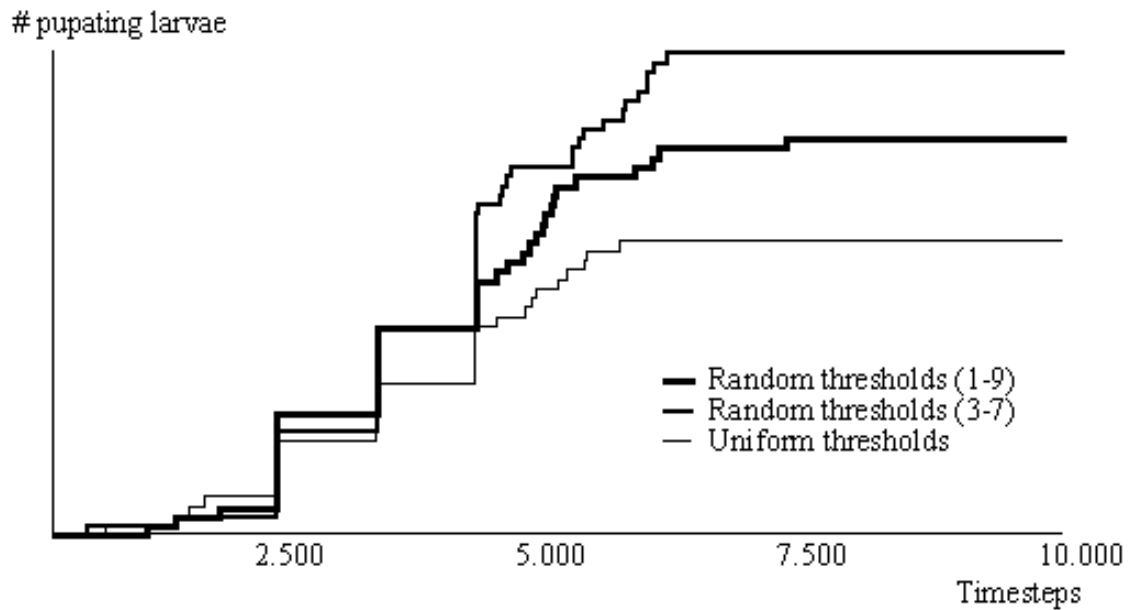


Figure 4: Average number of pupating larvae in 10 simulation runs.

small to survive over a realistic timespan. Real bee colonies contain a 1000 times more bees than the colonies in our simulation experiments. A

larger size may be crucial for the survival of the hive, especially since some group effects may not occur with too few individuals. The time the colonies were able to sustain themselves, however, varied considerably between runs.

6 Conclusion and Further Work

In our simulation experiments variability in activity selection thresholds resulted in a significant advantage for the bee colony. This occurred even though there was no increased efficiency in task performance through specialization of individual bees. This result shows the possibility that different dispositions to do certain tasks among individual bees might support the whole. The reason for this effect might be a more differentiated response of the colony to changes in conditions and to communication signals inside the hive. If variation in genetic predisposition among hive members results in improved performance of the colony, this also provides an explanation why honeybee queens mate with multiple males.

One problem with the model is that parameters are only partly derived from experiments with real bees, since not all data that were necessary to construct the model have been measured in honeybees. They should be optimized with respect to the output of eggs or pupating larvae and then again compared to data from the literature as well as new empirical data. With this optimization, we hope to get more realistic lifespans of our simulated colonies. Thus modeling and simulation experiments can give impulses for further research in the biological study of bees.

Another reason why the simulated colonies don't live very long might be their small size. Natural bee colonies contain many more individuals, typically between 6 000 and 60 000, and would not survive with 20 to 60 bees, which was the size of our modeled colonies. The task allocation mechanisms and the number of different tasks that are performed in a beehive might not be suitable for smaller colonies. Other species of bees, like for example bumblebees, do have smaller colony sizes, but little is known about their task allocation mechanisms. It is assumed that bumblebees are less specialized and that every individual performs all tasks in and outside the hive. Bumblebees also have fewer complex behaviors that require more than one bee: they don't directly exchange food (a behavior called trophallaxis), they don't have either the waggle dance, the tremble dance, or the shaking signal, and foragers deposit nectar themselves, making „food-storers“ unnecessary. Since the size of a

colony is likely to determine what kinds of group effects occur, we want to repeat the simulations with more individuals. Due to limitations of computer power, it might however be necessary to first simplify the model.

It can be assumed that, in addition to the effect of variation alone, bees learn to do tasks better with practice. By introducing a reinforcement mechanism we now want to model a natural feedback loop in which an animal improves its performance the more often it executes a certain action. Such a mechanism might come closer to approximating the processes in a real bee colony.

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