INDIVIDUAL BASED MODELLING OF TEMPERATURE INDUCED AGGREGATION BEHAVIOUR

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Abstract. There are several species of animals from different phyla that are known to exhibit diverse forms of social behaviour. Certain insect species like honeybees implement an interesting form of emergent social behaviour, based on a simple set of rules for individual behaviour rather than on complex cognitive interactions between individuals or with a leader. A good example for the bees' swarm behaviour is temperature induced aggregation. Young bees show a clear preference for temperatures around 36° C. If a group of bees is allowed to move freely on a ground exhibiting a two dimensional temperature gradient, their likeliness to come to rest in an area of preferred temperature is positively correlated to the number of interacting individuals up to a certain level. We suggested four different hypotheses to explain the basic mechanisms of this behaviour. In order to test them, we developed an individual based (bottom-up) NetLogo model which allows us to simulate a group of bees moving in a temperature gradient. By varying the influence of each of the four hypothetical mechanisms and comparing the result of the respective simulation to the results of real life experiments, we receive valuable clues to determine the likeliness of each hypothesis.

1 Introduction

Many species of social animals are confronted with the problem of controlling the interactions of a large number of individuals - a swarm - in a way that the entire community benefits from the individual behaviour. This is often achieved without the availability of a leader that could exert control over the individuals. Each individual acts in a way that can be described by a set of simple rules while being oblivious to the greater context of its community. Still, their interactions lead to emergent behaviour, allowing the collective (the swarm or the colony, in the case of social insects) to accomplish tasks that a single individual is unable to achieve. This is especially true for social insects, whose sensory equipment and central nervous information processing are comparably simplistic. Such emergent phenomena can lead to "swarm intelligent" decisions [1][2][3], where the group of agents is able to solve a problem collectively, while single individuals are unable to solve the same task in a comparable manner.

Eusocial bees like the European Honeybee (*Apis mellifera L.*) are known to accomplish a wide spectrum of tasks based on emergent behaviour, including the foraging for nectar and pollen and several "hive keeping" tasks like processing and storing of food, nursing of brood and collectively regulating the temperature in the hive.

Experiments with temperature organs by Heran showed [4][5], that honeybees exhibit a preference for specific temperatures which varies depending on their age. In these experiments, honeybees were released in a narrow metal-and-glass cylinder which was subsequently heated on one end and cooled on the other, thus creating a steep one-dimensional temperature gradient inside of it. In such a gradient, the honeybees always move to the section with their preferred temperature, which was found to be around 36° C for young honeybees. While single bees usually find the area of their optimal temperature in a temperature organ and rest there, more complex setups including a two-dimensional, flatter gradient seem to make it difficult for single bees to find a spot with their preferred temperature. However, when observing groups of bees in a heterogeneous temperature field we found a remarkable ability of larger groups to find the area of their preferred temperature and stay there by forming a cluster. Smaller groups or single bees were less likely to stay in this area.

We developed four different hypotheses on how this ability could correlate with the group size. The four basic hypothetical strategies are a strict uphill walk (*Type 1*) and a random walk combined with either continuous (*Type 2*) or occasional measuring of the local temperature, where occasional measuring would occur randomly (*Type 3*) or after a collision with another bee (*Type 4*). A type-1 bee would stop at a local optimum with a fixed probability, a type-2 bee would stop with a probability that depends on the local temperature. Bees of all types would remain at their location for a time that depends on the local temperature. We also consider the possibility of intermediate strategies consisting of any combination of basic strategies.

2 Model

In order to test the behaviour resulting from the suggested strategies, we created a *NetLogo* [6] model which allows us to model a group of bees moving in an arena with a deliberately designed temperature gradient. Our model was implemented as a multi-agent model [7][8], where every bee is represented by an individually acting agent. A set of basic behavioural parameters, most of which are adjustable in real-time, are applied to each bee at every time step. Another set of parameters allows for an on-the-fly adjustment of the surrounding environment. All important variables can be monitored via the interface and exported to files in different formats.

The model was developed and successfully tested under NetLogo 3.1.1, which was operated under Java VM 1.5.0_06. It is partially incompatible with earlier or later versions of NetLogo.

2.1 Environment

The environment consists of a rectangular arena which is composed of 36 x 20 patches, representing the arena of 34.3 x 18.5 cm that we used in our real life experiments. Every patch is characterized by its temperature and, based on its temperature, the pre-calculated probability for a bee to stop on it and the time for which the bee will rest after having stopping (see below).

The temperature of every patch is determined by the ambient temperature plus the combined effect of two heat lamps, which can be placed deliberately in the arena. The power of the individual heat lamps can be regulated at temperature level, and the lamps can be completely deactivated. A setting for the temperature attenuation on the ground determines the range of the lamps' effect and the slope of the temperature gradient. In order to be able to simulate inaccuracies in the bees' ability to measure the temperature, the temperature of every patch can be blurred by an optional noise-function, for which frequency and amplitude can be adjusted.

The patch-specific probability for a bee to stop on it and the duration of the bee's ensuing rest are derived from the patch's temperature using either a linear function, a normal distribution or a sigmoidal function depending on the pertaining setting. Additional settings determine the maximum probability to stop and the maximum resting time as well as the slope of the function (linear and sigmoidal function) or the standard deviation (normal distribution). Settings for the optimal temperature and the bees' tolerance for departure from the optimal temperature influence both stopping probability and resting time in all three function types. Table 1 lists the exact formulas applied to the function types.

Function type	Stopping probability	Resting time
Linear	$P(T)=max\{0,P_{max}-\lvert T_{opt}-T\rvert\cdot k\}$	$t(T)=max\{0,t_{max}-\lvert T_{opt}-T\rvert\cdot 300\text{k}'\}$
Normal distribution	$P(T)=\frac{P_{max}}{\sigma\cdot\sqrt{2\pi}}\cdot e^{\frac{-1}{2}\cdot(\frac{T-T_{opt}}{\sigma})^2}$	$t(T)=\frac{t_{max}}{\sigma'\cdot\sqrt{2\pi}}\cdot e^{\frac{-1}{2}\cdot(\frac{T-T_{opt}}{\sigma'})^2}$
Sigmoidal	$P(T)=\frac{P_{max}}{e^{(\lvert T_{opt}-T\rvert\cdot 10k)}}$	$t(T)=\frac{t_{max}}{e^{(\lvert T_{opt}-T\rvert\cdot 10k')}}$

Table 1: The three available types of functions for stopping probability and resting time ***T*** represents the temperature of the patch, $\boldsymbol{T_{opt}}$ the optimum temperature. $\boldsymbol{P_{max}}$ and $\boldsymbol{t_{max}}$ describe the maximum probability to stop and the maximum resting time, respectively. ***k*** and ***k'*** determine the slope of the respective function, ***σ*** and ***σ'*** the standard deviation of the distribution.

2.2 Agents

The agents of the model, the bees, are released to the arena either at a deliberate location or with a random distribution throughout the arena. A number of general behavioural parameters are applied to each of the bees at every simulation step. At every simulation step, each bee carries out one step of a random walk unless it is performing an uphill step (see below), in which case it would move towards the best neighbouring patch or rest in a local optimum. The random walk is controlled by the following parameters:

- *Maximum speed*: This parameter determines the maximum speed in cm/s a bee can achieve. In the simulations described in this paper, all bees invariantly move with maximum speed.
- *Stopping probability*: For a *type-1* bee, this parameter determines the bee's probability to stop and rest when it resides on a patch with optimum temperature. For a *type-3* bee, it determines its probability to stop spontaneously and subsequently measure the temperature of its patch. This parameter is not applicable to *type-2* and *type-4* bees (refer to Table 2 for a description of the behavioural types).
- *Turning probability*: This parameter determines the probability for a bee to make a turn during its random walk.
- *Maximum turning angle*: This parameter determines the maximum angle by which a bee can turn at once during its random walk.

The four hypothetical behavioural strategies described above are represented by four parameters that allow us to adjust the influence that each of the strategies has on the bees' ultimate behaviour. The contribution of each of the strategies towards the ultimate behaviour is adjusted in the form of the percentage of simulation steps at which a behavioural decision following the rules of a specific type is performed. Table 2 lists the descriptions of the four behavioural strategies and their implementations in the model.

Behavioural strategy	Implementation in the model
Type 1 Strict uphill walk	The bee walks uphill in the temperature gradient. When arriving at a patch with optimal temperature it stops with probability = "*Stopping probability*" and rests for ***t*** seconds.
Type 2 Random walk, continuous measuring	The bee moves in a random walk and performs a temperature measurement at every simulation step. It stops with probability ***P*** and rests for ***t*** seconds.
Type 3 Random walk, Random measuring	The bee moves in a random walk and occasionally stops with probability = "*Stopping probability*". After stopping, it measures the temperature of its patch and then rests for ***t*** seconds.
Type 4 Random walk, Collision induced measuring	The bee moves in a random walk. If it collides with another bee it stops with probability ***P***, measures the temperature of its patch and rests for ***t*** seconds.

Table 2: Implementation of the four hypothetical strategies in the model "*Stopping probability*" is a general behavioural parameter (see above), ***P*** and ***t*** are patch-specific parameters that are pre-calculated based on the patch's temperature (See Table 1 for a detailed description of the functions).

Any bee in the arena can be designated as a focus animal (an agent of interest), which can be individually tracked during its walk through the arena. For every simulation step, the temperature of the bee's patch, the departure from the optimum temperature, its current walking speed and the behavioural strategy that was applied to the bee at the current simulation step are recorded and optionally saved to a file (see below). For quick evaluation and for presentation purposes, the bees' trajectories can be optionally drawn as they move through the arena. The trajectories make it easy to quickly identify highly frequented areas of the arena.

2.3 Simulation

Every simulation run is preceded by an initialization of the internal simulation parameters and of the environment. After this procedure, the simulation can be operated in pause mode, allowing for further adjustment of the user configurable simulation parameters while observing the effects on the environment of any changes that are made. The actual simulation of the bees starts when the pause mode is deactivated.

Once started, the simulation runs until it is either halted by the user or at least one of several optional stop conditions is met. Stop conditions are met when either a certain number of bees have arrived in the optimum or in the warmest third of the arena or after a certain period of simulated time has passed.

A setting for the simulation time covered by a single simulation step allows for the regulation of the simulation time's granularity. Since all time dependent behavioural parameters relate to simulation time rather than to simulation steps, this setting allows us to balance execution speed and precision according to our needs.

During the simulation, important collective data and data about individual bees can optionally be recorded.

If focus bees have been selected, their local temperature and walking speed as well as the behavioural strategy which has been applied to determine their behaviour at the current simulation step are recorded. Additionally it will be remembered for each focus bee which other bee, if any, it has collided with at the current simulation step and to which cluster, if any, the focus bee belongs.

Separate from the focus bees, the current location, local temperature and walking speed as well as the currently applied behavioural strategy can be recorded for each bee in the arena.

The collective data, which are gathered independently from the individual data, consist of the percentage of bees located in the optimum, in the warmest third of the arena and in areas that are either below or above the tolerable optimum temperature, the percentage of walking and clustering bees and the size of the biggest cluster at the end of each sampling interval. The sampling interval can be selected at the start of a simulation run.

Data about individual bees can optionally be saved to files in csv-format, collective data to either a file in *csv*-format or in "*Noldus Observer*"-format [9]. The latter file format is used by a program frequently used in the field of ethology to analyse behavioural data of animals. This allows us to carry out an automated comparison of simulated agents' behaviours with real animals' behaviours. The *csv*-files contain an automatically generated summary section, thus allowing for a fast and easy evaluation of the data gathered during a simulation run.

3 Methods

In order to test the validity of the model we carried out a number of simulation runs and compared the behaviour of the simulated bees to the behaviour of real bees as observed in real experiments. While many parameters like walking speed and turning angle could be estimated from real observations, some other behavioural parameters had to be tuned deliberately in order to enable the model to deliver results close to reality.

After establishing the simulation parameters, we carried out single simulation runs with varying numbers of bees and compared the final results of the simulation to those gained from similar real experiments.

Our real experiments were carried out using freshly emerged (less than one day old) European honeybee workers (*Apis mellifera carnica*), which were released into an arena of 34.3 x 18.5 cm. The ground of this arena was formed by a wax comb, on which we established a temperature gradient using an infra-red heat lamp which we positioned above the left edge of the arena. Once the gradient was sufficiently stable, we released bees at the right edge of the arena and observed their behaviour with the help of a video camera operating under infra-red light. Infra-red light is invisible to bees, thus we can exclude an influence of optical clues on the bees' behaviour. The video signal was recorded on tape which was later digitized. The digital data was evaluated automatically and exact locomotion profiles could be retrieved for recordings of single bees.

With our simulations, we intended to answer the following questions:

1. Does the behaviour of single bees in the simulation tally with the behaviour of bees in a real experiment? We compared the trajectories of the real and simulated bees' movement in the arena to answer this question.
2. Does the clustering behaviour of groups of bees in the simulation tally with the one observed in real experiments? In order to answer this question, we compared the final frames of the recordings of our real life experiments with groups of bees to those of our pertaining simulations.
3. How do existing clusters react when a heat lamp is turned off and another lamp at the opposite edge of the arena is turned on? We positioned two heat lamps above the far edges of the arena, turned on the left one and released a number of bees near the right edge of the arena. We then waited for a cluster to form beneath the left heat lamp and then switched it off and turned on the right lamp. Finally, we compared the behaviour of the simulated clusters to the one of clusters in real experiments.
4. What is the correlation between group size and the ability to form stable clusters in an area of optimal temperature? We answered this question by carrying out a number of experiments with different group sizes using NetLogo's "BehaviorSpace" tool. This tool provides a simple interface for repeated execution of a simulation with varying parameters ("parameter sweeps", sensitivity analysis).
5. Does the locomotion behaviour of simulated bees tally with the one of real bees? We approached this question by comparing the individual behaviour of simulated bees to the one of single bees in real experiments. The behaviour of simulated bees was evaluated using the model's recording and exporting functions, the behaviour of the real bees was analysed using automated tracking of the digitized video recordings of experiments with single bees. In this case, the bee's location was determined in intervals of 1 second and their current walking speed was extracted from the data. We then compared the frequency of walking and resting in different temperature intervals.

All simulations were carried out with a temporal resolution of 0.1 s per simulation step. The optimum temperature was assumed to be 36.0 °C and the tolerance interval for the optimum temperature was chosen to be 1.0 °C. The bees' walking speed was invariantly 1 cm/s.

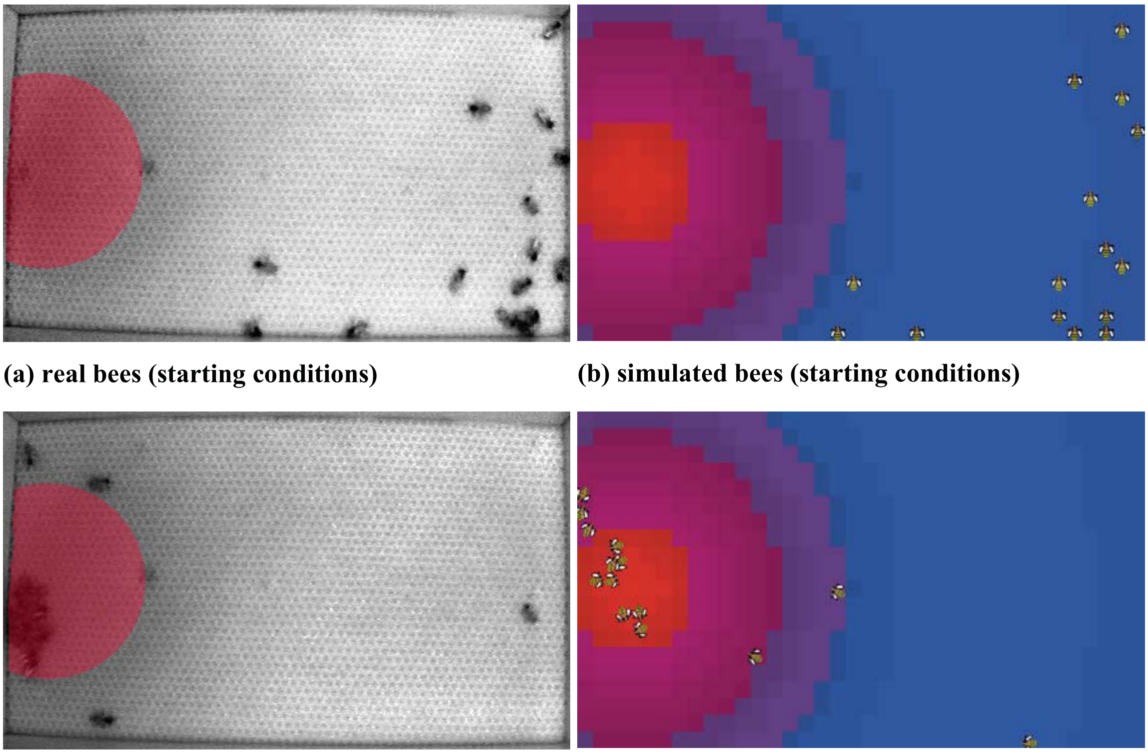
4 Results and Discussion

From our observations in real experiments, we know four distinct types of basic locomotion behaviour: Random-walking, goal-finding, wall-following and immobility. Most bees however exhibited intermediate forms of the four basic behaviours. We were able to reproduce the basic locomotion behaviours and typical intermediate forms by tuning turning probability and angle, general stopping probability and the parameters for the temperature dependent functions for stopping probability and resting time (see Table 1). Figure 1 shows a comparison of the trajectory of a real bee (a) and a simulated bee (b). Both real and simulated bees had a similar turning behaviour, resulting in comparable trajectories. However, the model could not reproduce spontaneities in the bees' behaviour like periodic changes in activity. Also, the behaviour of resting real bees was different than the one of those in the model. While simulated bees were completely inactive while resting, real bees often occasionally move or turn around. This behaviour could have an influence on cluster stability. This aspect of the model will be adapted accordingly in the future.

(a) trajectory of a real bee (b) trajectory of a simulated bee

Figure 1: Comparison of the trajectory of a real bee (a) with that of a model bee (b) The real bee (a) and the simulated bee (b) were moving for 10 minutes in a steep temperature gradient (real bee 30 - 37° C, simulated bee 26 - 36 °C). The optimum temperature area was located at the left side of the arena. The real bee's starting point is marked by an open circle, its end point by a filled circle. The simulated bee started on the right side of the arena and came to rest in the optimum area.

The clustering simulations yielded results that were usually very close to those gained in real experiments. Figure 2 compares the results of a single real experiment to those of a simulation with a similar setup. The positioning of the bees was similar in both instances, but there were three smaller clusters in the optimum area in the simulation where in the real experiment a single, bigger cluster existed. Clusters generally appeared looser in the simulation than in reality because of the fact that in the simulation, the rather large patches (1 cm²) cannot be shared by several bees. This will be remedied in future versions of the software by using a narrower grid of patches. Additionally, it was not possible to fine tune cluster dynamics sufficiently to exactly mimic the dynamics of real clusters. Apparently, this was due some of to the temperature dependent parameters which are invariant during the course of the simulation, while they could be subject to change over time in real bees. This caused the model to either produce realistic cluster formation, but too little cluster stability, or realistic cluster stability but accelerated cluster formation. A dynamic variation of the parameters in question will be a part of future versions of the model.



(a) real bees (starting conditions) (b) simulated bees (starting conditions)

(c) real bees (final conditions) (d) simulated bees (final conditions)

Figure 2: Comparison of the clustering behaviour of real and simulated bees (a) and (b) show the starting setup of a real experiment and a similar simulation run, (c) and (d) show the clustering resulting after 10 minutes. In both cases, a steep temperature gradient was used (real experiment 26 - 36° C, simulation 22 - 36° C). The area of optimum temperature in the real arena is marked by a red circle.

In our switching simulation, existing clusters beneath the active heat lamp reacted to the switching of the heat lamps by immediately dissolving and starting to move through the arena again, eventually forming a new cluster beneath the now active heat lamp at the right edge of the arena. Figure 3 shows the results of an exemplary switching simulation run in the form of a time line. In real experiments, clusters took a long time to dissolve after a heat lamp has been turned off. One probable explanation for this observation is that the lamp and the wax comb took some time to cool off, thus still providing sufficient warmth for the bees to remain resting. In addition, bees might have been reluctant to leave an existing cluster even when the environment became suboptimal. The clusters dissipated slowly when single bees started to leave them by moving through the arena and by coming to rest in the new optimum area, eventually forming a new cluster. The model's environmental physics do not take into account the inertia of heat lamps or the ground nor has a parameter for the bees' bias to remain in a cluster. Thus, the model has to be extended accordingly in order to be able to deliver realistic predictions about this aspect of clustering behaviour.

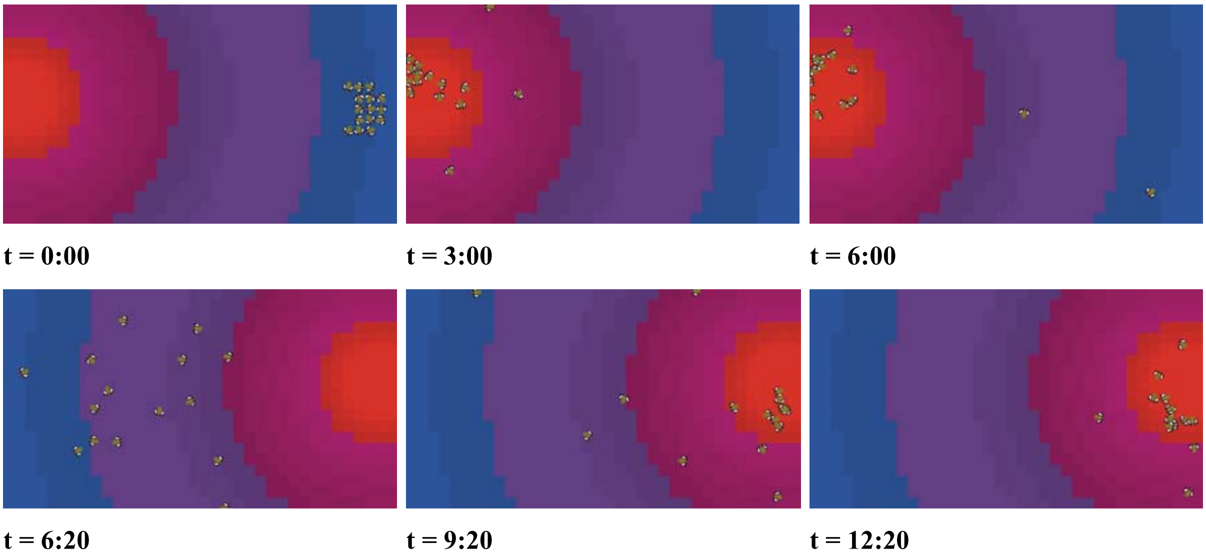


Figure 3: Time line of a simulation run of a switching experiment
The bees were released near the right edge of the arena (0:00). They moved towards the optimum area at the left and quickly formed a cluster (3:00). After 6:00 the heat lamps were switched and the cluster dissolved immediately (6:20). Again, the bees found the optimum area and quickly formed a new cluster (9:20). The arena exhibited a steep gradient (25 - 37° C).

In order to quantify the correlation between group size and the ability to form clusters in the optimum area, we compared the ratio of bees in the optimum area for different group sizes. Each group size was simulated 20 times and the mean ratio of bees in the optimum area was evaluated for different time intervals. The behavioural strategy selected for the bees in these simulations was exclusively *type-4* (random walk with collision induced temperature measuring). From the results, it is clear that the ability to find the optimum area and rest there is significantly correlated to the group size. The larger the groups were, the higher was the percentage of bees that found the optimum area. It also became clear that the bees reached the optimum rather fast (during the first 5 minutes) and usually stayed there (see Figure 4).

In addition, we analysed the average persistence of the largest cluster depending on group size. This relationship is characterized by a sigmoidal function (see Figure 5). While groups of up to 15 bees formed rather short lived clusters, groups of 20 bees formed clusters that lingered throughout the simulation run in 11 of the 20 experiments with 20 bees. Groups of 30 or more bees always formed clusters within the first 50 seconds that lingered throughout the experiment.

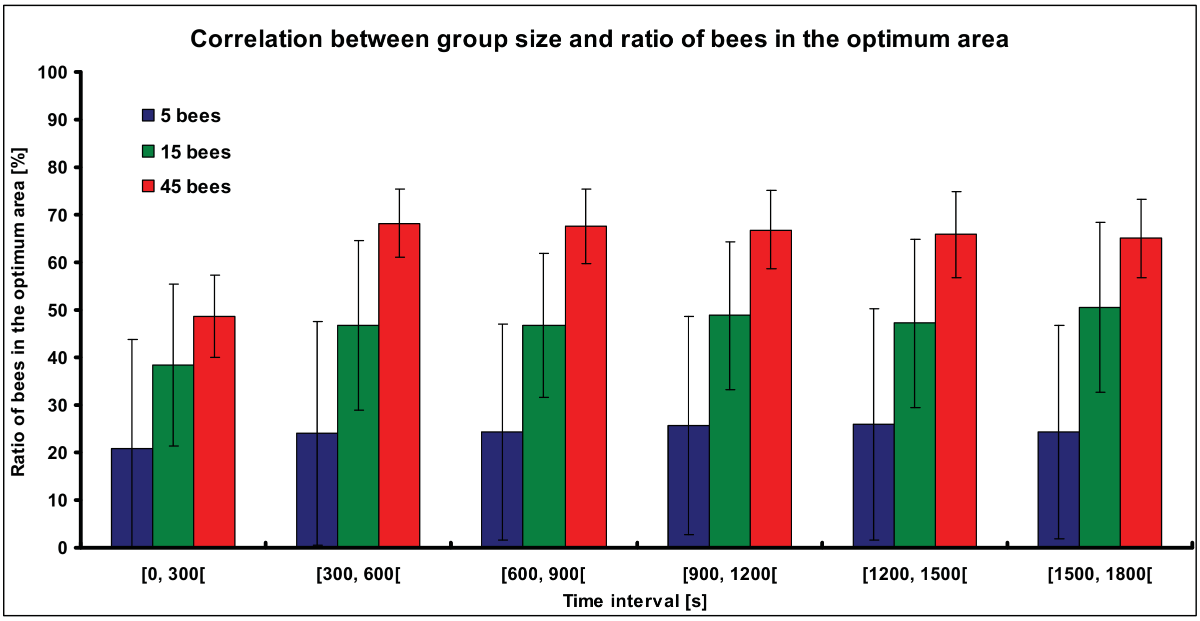


Figure 4: The correlation between group size and bees in the optimum area in different time intervals
20 simulation runs were executed for every group size. The mean percentage of bees in the optimum area during 5 minute intervals of the simulations is shown for each group size. The error bars show the standard deviation, which is bigger for smaller group sizes due to a greater influence of the individual's behaviour.

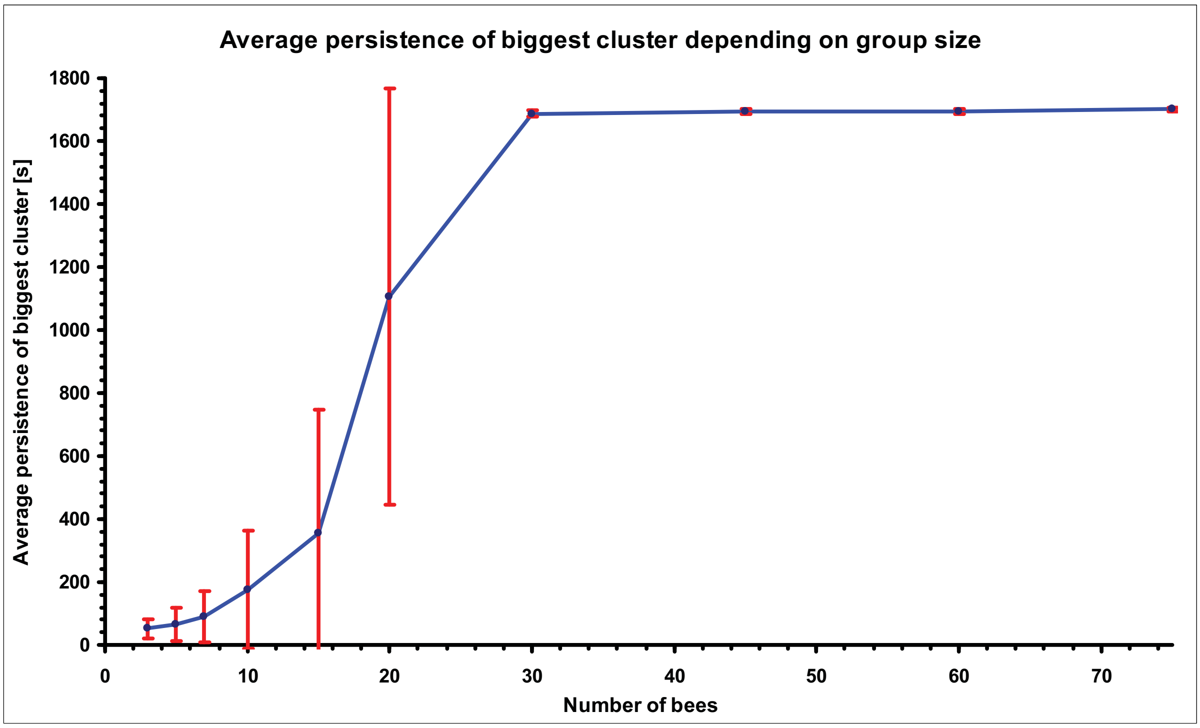


Figure 5: The dependency of the average persistence of the biggest cluster from the group size
The data were retrieved from 20 experiments with each group size (3, 5, 7, 10, 15, 20, 30, 45, 60 and 75 bees). The function represents the average time that the biggest cluster persisted before it dissolved. In experiments with up to 20 bees, several consecutive clusters were formed during an experiment. In the case of 30 or more bees, the biggest cluster, once formed, lingered for the entire remaining experiment. The dependency is characterized by a sigmoidal function whose saturation point is defined by 30 bees. The error bars represent the standard deviation.

The distribution of walking and resting behaviour in different temperature intervals was very sensitive to the distribution of the selected behavioural strategies. We carried out 20 simulation runs of 10 minutes each with single bees randomly placed in the arena. The distribution of behavioural strategies was 50 % *type-2* (continuous measuring of temperature) and 50 % *type-3* (random measuring). We did not achieve a close fit of the results of our simulations to the results of the observations from our real experiments. However, the distribution functions showed a similar development (see Figures 6 and 7), indicating that the simulated bees' behaviour has a correct tendency.

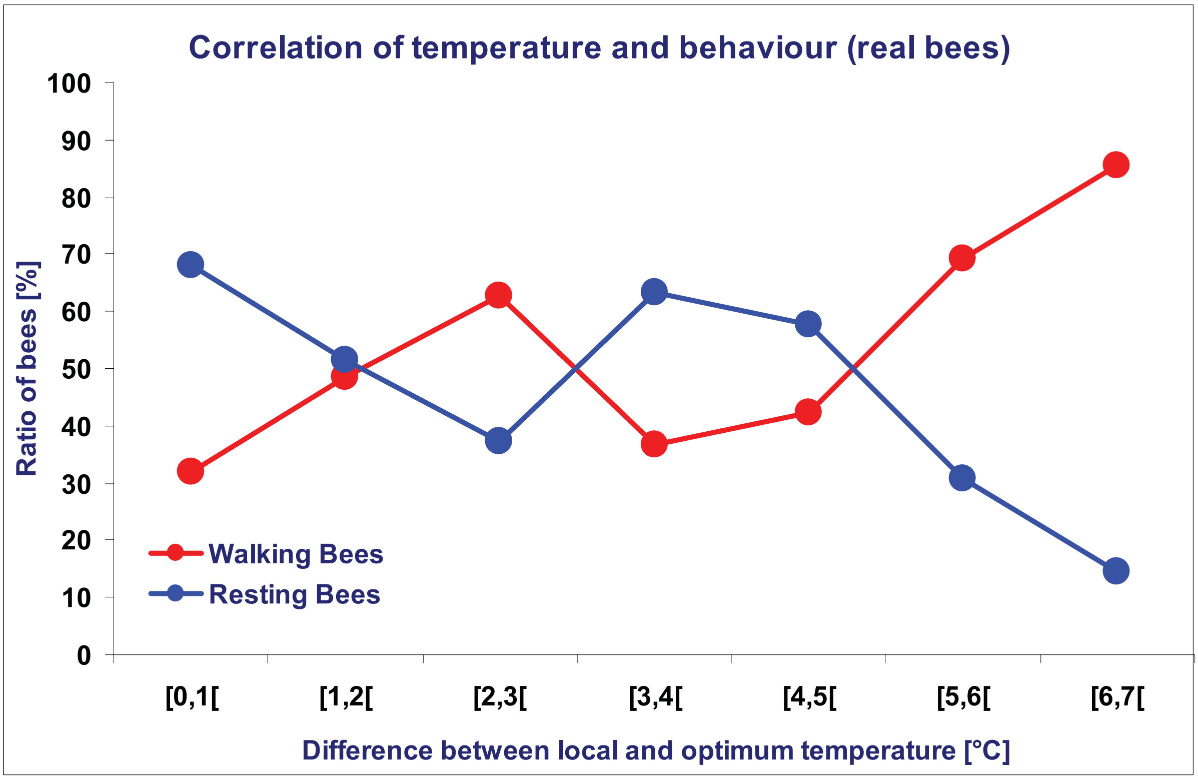


Figure 6: The frequency of walking and resting behaviour as observed in a real experiment The graph shows the percentage of bees walking and resting at different levels of temperature difference to the optimum. The result is based on 37 experiments with single bees moving for 10 minutes each in different temperature gradients.

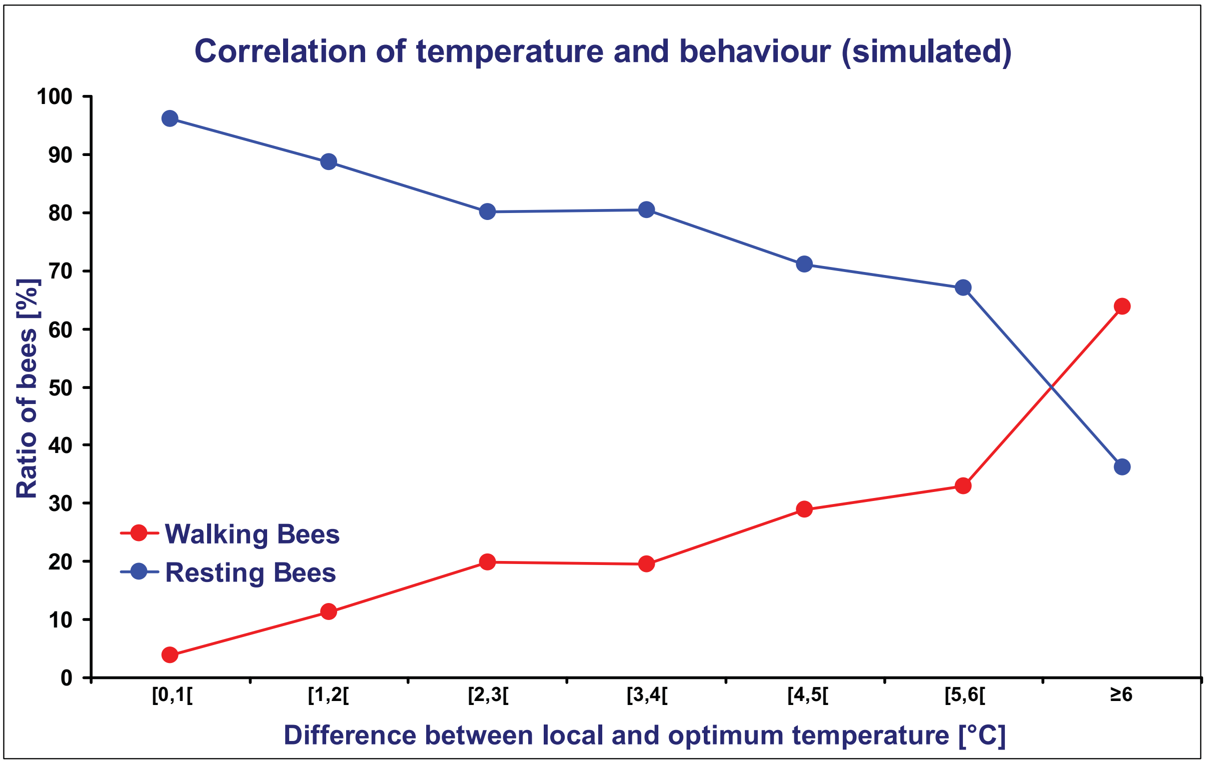


Figure 7: The frequency of walking and resting behaviour as predicted by the model The graph shows the percentage of bees moving and resting at different levels of temperature difference to the optimum. The result is based on 20 simulations of single bees moving for 10 minutes in a steep temperature. The distribution of behavioural strategies was 50% for *type-2* and 50% for *type-4*.

5 Conclusion

Our results showed that our model was able to describe the collective aggregation behaviour of young honeybees in a temperature gradient quite well. We could show by our model that the observed aggregation clusters and their positions are very likely governed by a set of simple rules, and can thus be interpreted as being "swarm intelligent" [1][2][3] collective decisions, although we found (also qualitative) differences when comparing data recorded from real animals with those from simulated agents. Nevertheless, in a majority of the cases, we found qualitatively similar patterns of emergent collective behaviour. In the future we will refine the multi-agent model and, additionally, investigate a more abstract macroscopic model (like one we already produced for a similarly acting robot swarm [10]), which will allow us to derive more generalized results.

6 Acknowledgements

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