MARTIN-LUTHER-UNIVERSITÄT
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Modelling of temperature effects on honeybee colony performance

1.) Purpose of the visit

General subject

Division of labour and temporal polyethism in honey bees

Eusocial insects are characterised by a highly sophisticated division of labour among the members of the colony, resulting in individuals specialised in different tasks. In honey bees, division of labour is realised by a temporal polyethism and the tasks performed by a worker change with age, starting with inhive activities (like cell cleaning and brood care) and ending with foraging outside the hive. However, this mechanism of task allocation does not follow a rigid pattern, but allows for flexible responses in dependence of environmental and intranidal requirements, which may even reverse the behavioural development from outdoor to indoor worker.

Regulation of hive temperature

Another amazing feature of the honey bee colony is the ability to regulate the temperature and climate in the hive. Especially the temperature sensitive larvae and pupae are exposed to a precise temperature control leading to brood temperatures from 32°C to 36°C with a mean of 34.5°C. To maintain the temperature within this range, worker bees can cool the hive by fanning and evaporation of water or heat it by “shivering” of their flight muscles thereby generating metabolic heat. In addition, the workers can regulate the temperature through clustering behaviour. Tightening of the cluster reduces thermal conductance and increases thermal insulation, whereas loosening of the cluster will facilitate the cooling of the nest. The increasing number of workers in the colony over the season as well a seasonal climate variations will therefore be an important factor in understanding the dynamics of brood nest temperature.

Influence of brood temperature on the behaviour of adult bees

In spite of the accurate temperature control in the hive, the variation in brood temperature is sufficient to affect the behavioural performance of the adult bees. Workers experienced higher temperatures during their pupal development show an increased dancing activity and better memory abilities (Tautz et al. 2003). They also exhibit an accelerated behavioural and physiological development, leading to precocious foraging and a reduced life expectancy (Becher et al. 2008, Becher and Moritz 2008a).

Aims of the project

Simulation model

The aim of the project was to develop a computer model of a honeybee colony, including the population dynamics of the colony, heating of the broodnest by adult workers, foraging activities and the environmental factors nectar supply and ambient temperature. We were interested to analyse the consequences of variation in the pace of behavioural development on the organisation of the colony. This variation was caused either by differences in the developmental temperature or by random, individual variation.

<u>2.) Description of the work carried out</u>

Under supervision of Prof. Dr. Charlotte Hemelrijk, I developed an individual based computer model of a honey bee colony. The model was implemented in Delphi (Pascal) and comprises mainly the population dynamics of the colony, the temperature distribution in the broodnest, the foraging activities of the workers and the environmental factors ambient temperature and nectar supply (Fig. 1).

Model description

The brood develops from egg to larva to pupa, with a mortality and duration of the development depending on their cell temperatures. New emerged workers stay in the hive and might heat the broodnest, whereas older workers become foragers. The decision if a worker performs a task or is resting depends on individual threholds and environmental stimuli. Thresholds for heating are fixed, thresholds for foraging decrease with the age of an individual. The slope of the age dependent decrease of the foraging thresholds can be influenced by the pupal developmental temperature and random variation (Fig. 2). Bees developed under higher temperatures earlier become foragers. Adult workers have a daily chance to die, which increases with their foraging activities. The number of heating bees in each timestep defines the temperature distribution in the broodnest. The honey storage of the colony results from the nectar influx due to successful foraging and the energy consumption by feeding and heating.

Simulation runs

We varied four parameters for the analysis: ambient temperature, nectar supply, influence of random variance and the influence of brood temperature on the pace behavioural development (Tab. 1). For each of the 144 parameter combinations, 20 replicates were performed, summing up to 2880 simulation runs in total.

The ambient temperature influences the brood temperature of the individuals, the heating costs for the colony and the motivation of the foragers to fly out. The nectar supply represents the number of flowerpatches and the sugar concentration of the nectar. The influence of brood temperature describes, how strong the pace of behavioural development of the adult bees is affected by the developmental temperature during their pupal phase. A value of 0 means that brood temperature does not affect the pace of behavioural development at all (hot and cold bees start foraging at the same age), a value of 1 equals the measured empirical effect (earlier onset of foraging for bees developed under higher temperatures), a value of 2 represents an effect twice as strong as the actual empirical effect. The random variation adds a normally distributed variation to the slope, which defines the age-dependent foraging threshold and hence slows down or accelerates randomly the pace of behavioural development of an individual (Fig. 2).

Tab. 1: Tested parameter values.

Ambient temperature:	14°C – 16°C – 21°C
Nectar supply:	medium – high
Influence random variation:	0 – 1 – 5
Influence broodtemperature:	0 – 0.5 – 1 – 1.5 – 2 – 3 – 4 – 5

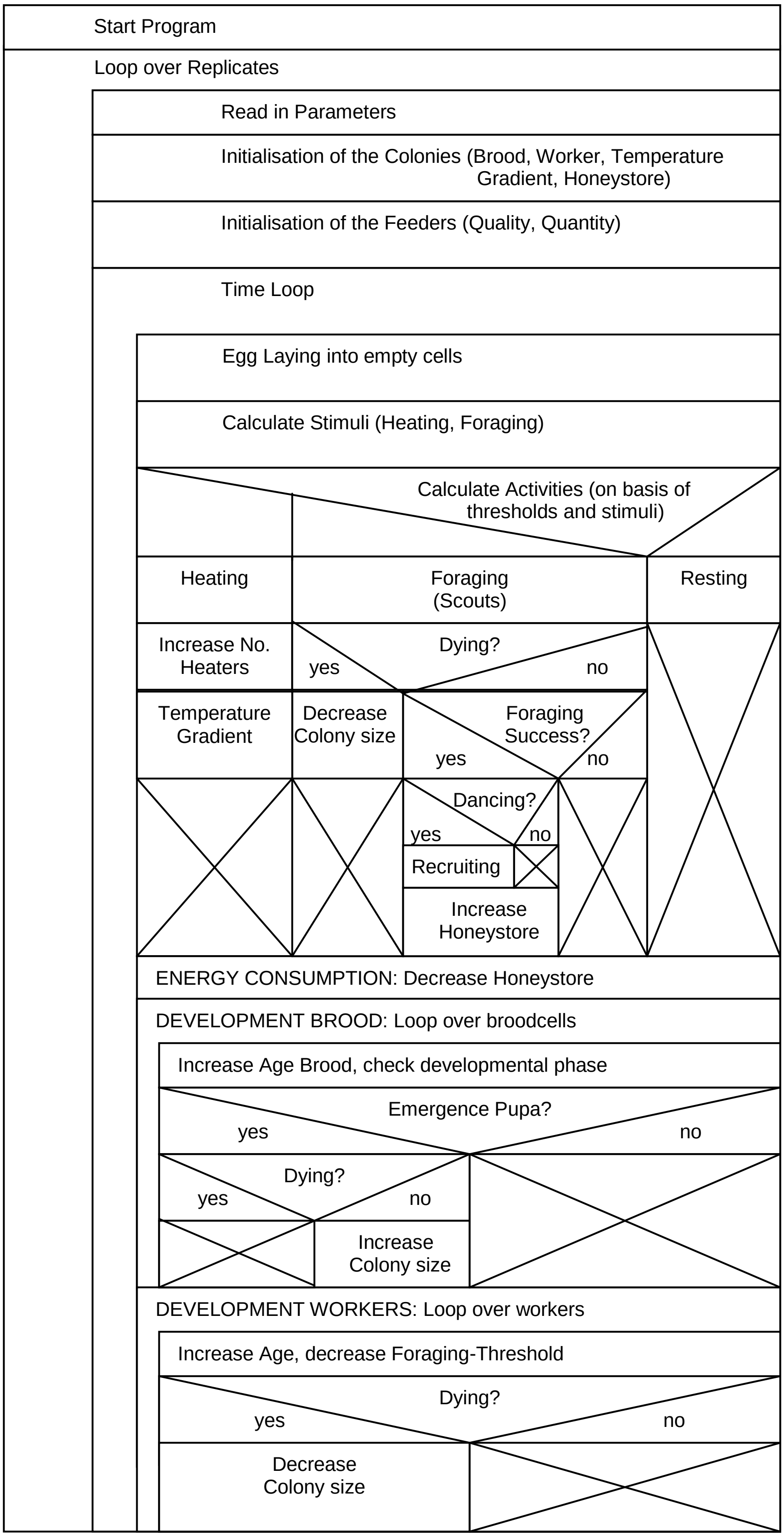

Fig. 1: Simplified overview of the model's structure.

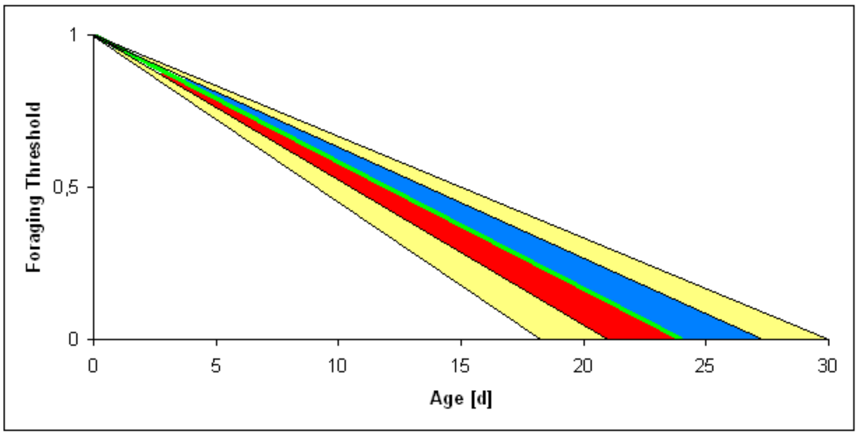

Fig. 2: A worker starts foraging, if the foraging stimulus is higher than the threshold. The foraging threshold decreases with the age of the worker. Bees developed under brood temperatures higher than 34.5°C (red area) show a faster behavioural development, whereas bees developed under cooler temperatures (blue area) stay longer in the hive. Additional, random variation can also be included into the model (yellow area).

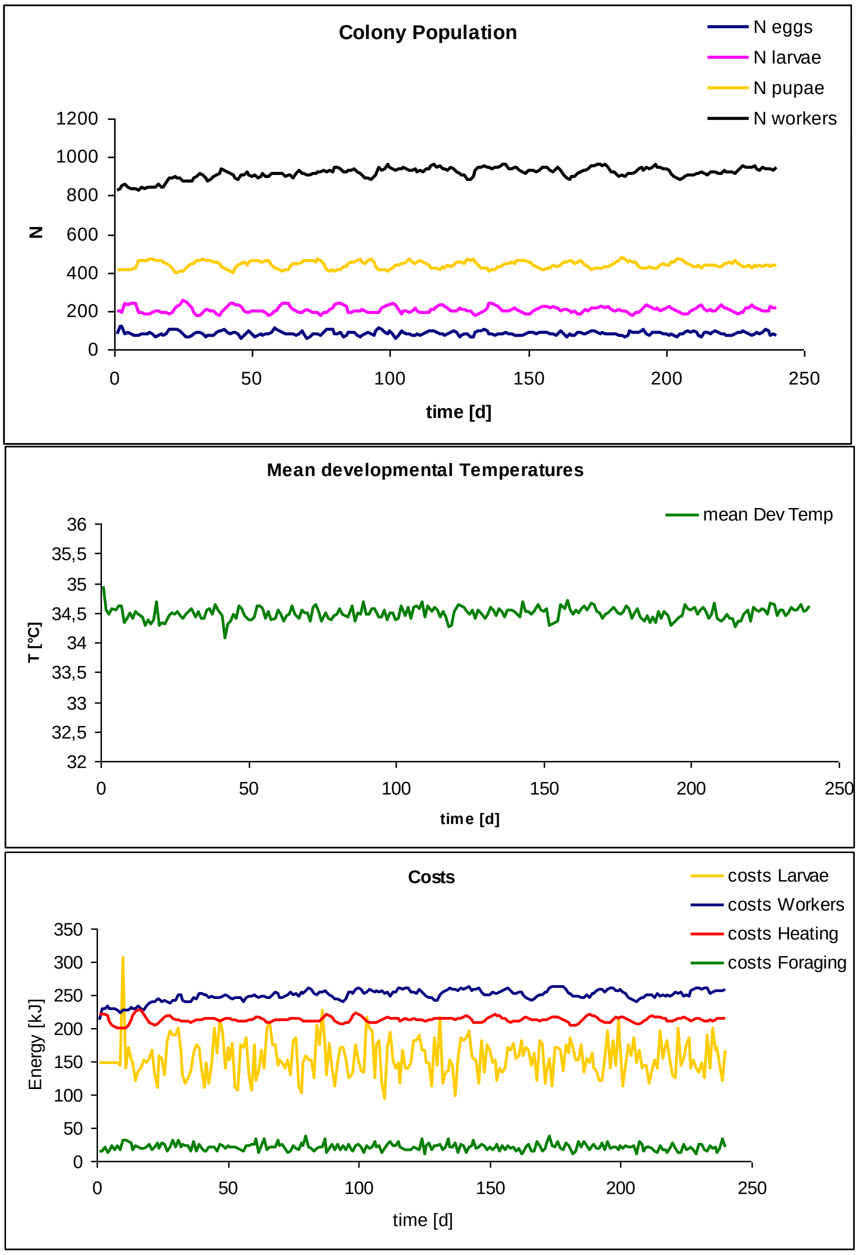

Fig. 3: Population size, mean developmental temperature and energy consumption (ambient temperature: 16°C, nectar supply: medium, genetic variance: 0, influence broodtemperature: 0)

<u>3.) Main results</u>

General results

We were able to parameterise our model in a way, that a realistic population dynamic arises. A broodnest size of 768 cells results in a population size of adult workers of about 900 bees (Fig. 3a). The mean developmental temperature is around 34.5°C (Fig. 3b), with extreme values between 32.5°C to 36°C.

Influence of brood temperature on colony efficiency

In the cool (14°C) and normal (16°C) temperature scenarios, we found no significant effect of the influence of brood temperature on the organisation and the honeystore of the colony. Irrespective if the behavioural development of the adult workers is affected by their brood temperature or not, those colonies possess all the same amount of honey storage in the end of the simulation. Under 21°C however, colonies profit if the brood temperature influences the pace of the behavioural development (Fig. 4). The stronger this effect is, the more honey is collected. Those colonies also show the ability to regulate the brood temperature closer to the 34.5°C-optimum (Fig. 5). Due to an earlier onset of foraging in bees developed under higher temperatures, a negative feedback loop arises, which stabilises the broodnest temperature (Fig. 6).

Influence of random variation

Although variation in thresholds is often assumed to be an advantage for an efficient division of labour in a colony, we found no significant influence of random variation on colony performance or nectar influx in our model. The colonies did not benefit from a random variation in the pace of individual, behavioural development.

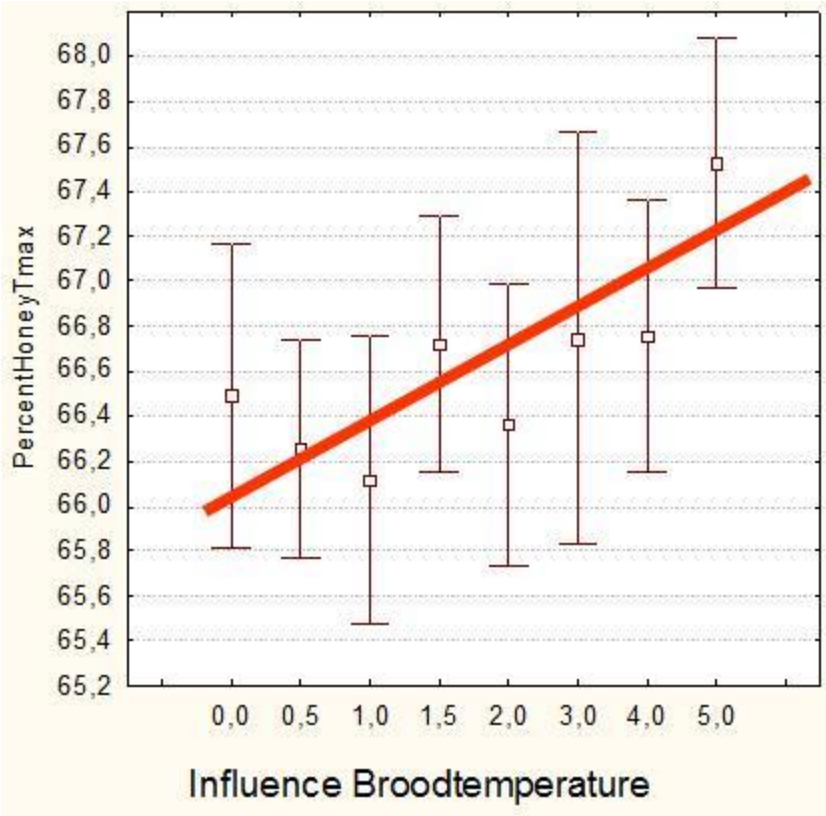

Fig 4: Under higher ambient temperatures, the honey storage of the colonies in the last timestep increases with an increasing influence of brood temperature on the behavioural development of the adult bees (ambient temperature: 21°C, genetic variance: 0, nectar supply: medium; Spearman-Test: $p<0.05$, $N = 160$).

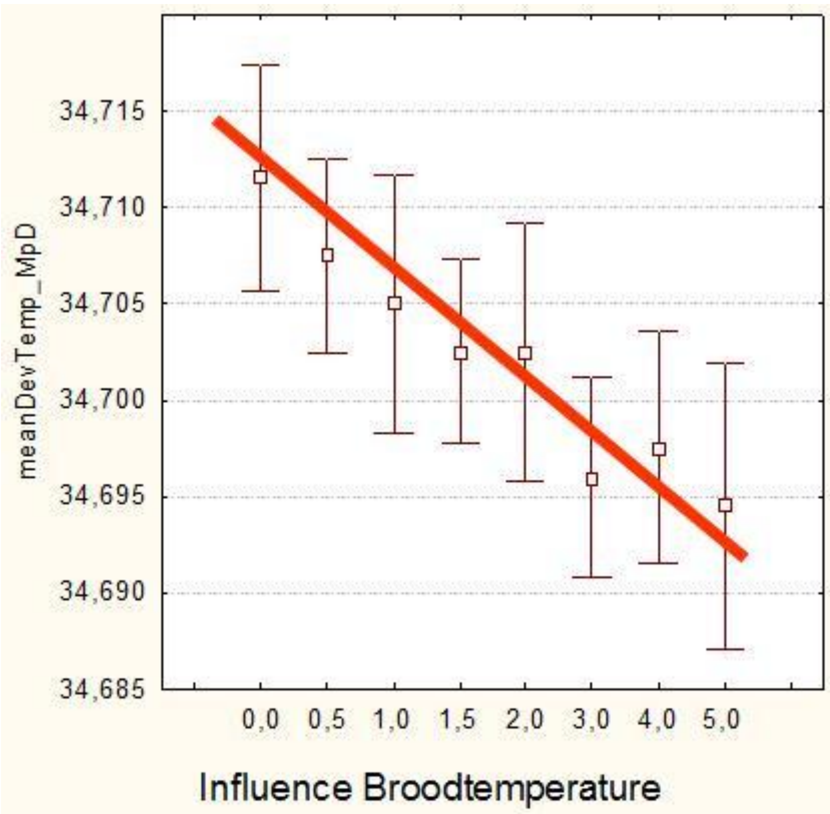

Fig 5: The mean developmental temperatures are closer to the optimal temperature of 34.5°C in the high temperature scenario, the stronger the influence of brood temperature on the behavioural development is (ambient temperature: 21°C, genetic variance: 0, nectar supply: medium; Spearman-Test: $p<0.0001$, $N = 160$).

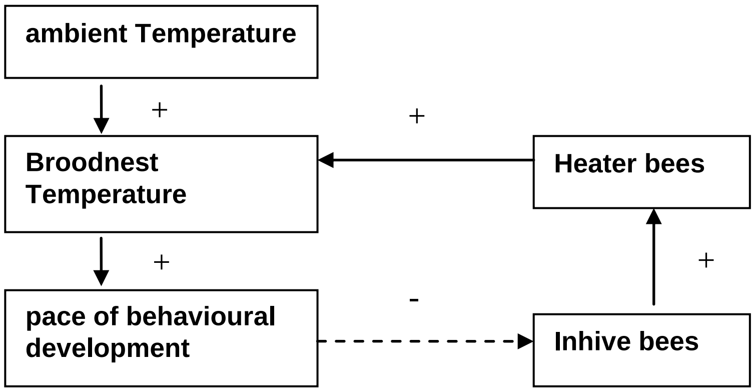

Fig. 6: A negative feedback-loop stabilises the brood-nest temperature

Conclusions

The results of our analyses suggest that it might be adaptive for honey bees to use an environmental factor like temperature as a fine tuning mechanism for the regulation of division of labour. In the warm temperature scenario, those colonies benefit from the accelerated behavioural development which results in a higher proportion of foragers and an increased honey store. Whereas in the cold and normal tempered scenario, those colonies did not have a significant disadvantage. Although this effect is small in our simulation, it might be of relevance also in natural colonies. Our model does not include a correlation between temperature and nectar supply, an effect that is usually given under real conditions. In this case, the benefit for colonies producing more foragers in warmer periods when more nectar is available would even be stronger than it is in the model.

The effect of an individual, random variation in the pace of the behavioural develoment, is negligible in our model. Variation in the decrease of foraging thresholds leads to an increased variation in the age of first foraging among the workers, yet this random variation had no significant effect on the colony performance and energy input. Colonies did not benefit from an increased random variation in the foraging thresholds.

We conclude that honey bees, due to their advanced abilities of temperature control in the hive by heating and fanning and the self-organised process, regulating the proportion of foragers and inhive bees, seem to be quite robust against changes in the ambient temperatures. Nevertheless, under certain circumstances, ambient temperature can influence the division of labour in the colony. In case of a possible climate change, honeybee colonies might even benefit if ambient temperatures increase.

4.) Future collaboration

We plan to continue the collaboration with Prof. Dr. Charlotte Hemelrijk. I will visit the Theoretical Biology Group in Groningen four times in the next months. The purpose of the visits will be to further improve the simulation model. We will model the broodnest temperature spatially explicit and add competition between two colonies.

5.) Projected publications

We currently work on a manuscript, dealing with the here presented data.

6.) References

Becher M, Scharpenberg H, Moritz RFA (2008) Pupal developmental temperature determines foraging specialisation of adult honeybee workers (*Apis mellifera* L.). Behav. Ecol Sociobiol, submitted

Becher M, Moritz RFA (2008a) Varying life expectancies in honey bee workers developed under different temperature regimes. Apidologie, in prep

Tautz J, Maier S, Groh C, Rössler W, Brockmann A (2003) Behavioral performance in adult honey bees is influenced by the temperature experienced during their pupal development. Proc Natl Acad Sci 100:7343-7347