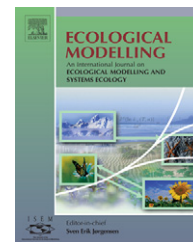


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HoPoMo: A model of honeybee intracolony population dynamics and resource management

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ABSTRACT

The population dynamics of eusocial insects differ significantly from those of non-eusocial animals. With eusocial insects, one has to distinguish between a population of colonies and the population of individuals inside each colony. These two levels are closely related, because the decision whether a colony reproduces or not is mainly determined by its intracolony population and resource status. In addition, a population's rate of colony mortality is strongly dependent on each colony's intracolony status. Honeybees collect their food in the environment, their most important ecological aspect is the pollinating of plants. In recent empirical studies, we demonstrated the importance of food supply on the population dynamics of honeybee colonies. In addition, honeybees show division of labor, which occurs in the form of age polyethism, meaning that morphologically almost identical worker bees choose their tasks mainly dependent on age. This task selection system is very flexible and is significantly affected by changes in task-specific workloads or in the age structure of the colony. Recent studies have shown that environmental factors and/or natural or experimental changes in resource supply heavily affect the age structure, resulting in changes in task allocation within the colony. These changes further affect the intracolony population dynamics and age structure. This situation can be described as a set of delayed feedback loops. We created a mathematically simple honeybee population model (HoPoMo) using difference equations to model the population dynamics and the resource dynamics of a honeybee colony. Our model emphasizes the importance of pollen supply and of brood cannibalism, an aspect that was neglected by other honeybee population models so far. HoPoMo includes simple models of task selection and of nutrient allocation. It allows us to simulate a variety of colony conditions (colony size, intrinsic bee characteristics, resource status) and a variety of environmental conditions (rain, temperature, botanical resource availability). The model can be easily parameterized with real weather data and with experimental colony treatments, so that we can use the model to interpret empirical experimental data. We successfully compared the predictions of our model with data gained from the literature and from own experiments. Extensive sensitivity analysis revealed that the model's predictions of population dynamics are very stable, except at very low mortality rates. And finally, we demonstrate, that the model can be used for several environmental conditions of honeybee living: controlled bee hives, scientifically used colonies and wild-life honeybees.

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1. Introduction

Honeybees are of enormous ecological importance as pollinators, mainly due to their fascinating ability to exploit food sources rapidly by recruiting masses of foragers. The population dynamics of honeybees are affected by environmental conditions (weather, pollen supply) and by colony-intrinsic factors (food stores, population of adult bees and brood, parasites). Thus, the understanding of the population dynamics of a honeybee colony was researched for almost 70 years now, driven by the aim to serve ecologists, bee-keepers and scientists.

In all eusocial insect species, population dynamics occur on two different levels: on the colony-level (number or density of colonies) and on the intracolony level (number of individuals within each colony). In honeybees, reproduction on the colony-level is achieved by swarming; the old queen leaves the nest with a fraction of the worker bee population and with a small part of the food resources (honey/nectar). The swarm founds a new nest in a new location, while the old colony continues its life with a new queen. In the best case, both colonies survive, leading to reproduction of a superorganism. For modeling the population dynamics on the colony-level, the factors “reproduction rate” (r) and “mortality rate” (m) apply to colonies, not to individual organisms, as with non-eusocial animals. The reproduction rate is the net number of swarms per year, while mortality rate expresses the survival of colonies throughout a year. What links such a colony-level approach to the population dynamics on the intracolony level is the fact that both reproduction rate and mortality rate are closely linked to the intracolony status of the colony. The more adult bees there are, the more sealed brood and nutrient stores are available in the colony in spring, the higher is the ability of the colony to swarm. Strong colonies are even able to produce several swarms per season. One of the main risks for a honeybee colony is survival throughout winter. Also, an optimal number of bees in autumn and a high level of food resources maximizes a colony's chance to survive winter. The number of new queens, which are essential for reproduction on the colony-level, is also controlled by the worker bees and is known to be strongly dependent on the intracolony population size.

In a honeybee society, almost all offspring are produced by a single queen. Therefore, population dynamics differ significantly from those of non-eusocial animals, where more (sometimes almost all) adult individuals reproduce and build up the population. Although the queen produces the colony members, her egg laying behavior is strongly influenced by other factors. There is a typical season-dependent pattern in the queen's egg laying rate: the queen produces very few eggs per day in winter and up to 2000 eggs per day in summer (Bodenheimer, 1937), and the worker bees in the colony regulate the amount of brood in strong dependence on outside factors (weather, food, influx) and of the intracolony status. Workers control the number of brood via cell preparation, which regulates the egg laying of the queen, and via cannibalism of larvae (Schmickl and Crailsheim, 2001), which leads to a recycling of proteins already invested into the brood (Webster

and Peng, 1987; Webster et al., 1987; Schmickl and Crailsheim, 2001). Survival rates of the brood strongly depend on the number of available worker bees (Eischen et al., 1982), on the season and weather (Woyke, 1977; Dustmann and von der Ohe, 1988), and on the resource status of the colony (Newton and Michl, 1974), because larvae need to be frequently fed by nursing bees (Haydak, 1963a) with proteins, carbohydrates and fat (Haydak, 1970). The larvae are fed by the nurses by a special fluid food (“jelly”) that is produced by the hypopharyngeal glands of nurse bees, the nutrients for the jelly are mainly derived from pollen (Moritz and Crailsheim, 1987; Crailsheim et al., 1992). Normally honey and nectar (which are the main carbohydrate sources) are plentiful within a colony, in contrast to pollen (the main protein source). Thus, the main factor determining brood rearing efficiency is the amount of available pollen in the hive (see Blaschon et al., 1999 for data). Schmickl et al. (2003) showed the dependency of brood nursing on the amount of stored pollen; Schmickl and Crailsheim (2002) demonstrated that the ratio of the amount of pollen to the number of larvae has a strong influence on brood nursing.

Another key issue in the understanding of honeybee colonies is the fact that honeybees have evolved age polyethism (Lindauer, 1952; Sakagami, 1953; Seeley, 1982), a system of age-based division of labor and task partitioning (Anderson and Ratnieks, 1999; Ratnieks and Anderson, 1999). Changes in brood production not only influence the size of the population, they also influence age demography and thus affect the division of labor. Also, the division of labor in turn influences age demography, because certain tasks involve higher mortality or markedly influence longevity.

Based on these recent empirical findings, we made the following assumptions on the mechanisms that regulate the population dynamics within a honeybee colony:

- (1) The honeybee queen produces eggs in a characteristic seasonal pattern. The maximum number of eggs produced in the maximum-peak season depends mainly on the queen's age, but also on the comb space that is available for egg laying.
- (2) The life tables of the bees are mostly seasonally fixed, thus the egg laying pattern of the queen results in a predictable age-demography of colony members, if the colony faces optimal conditions.
- (3) Despite this seasonality, the longevity of bees and the survival rates of several brood stages depend strongly on colony conditions (e.g., pollen supply, nurses-to-brood ratio).
- (4) These colony conditions can change over time due to changes of environmental conditions (weather). They can also change suddenly due to events like colony manipulations (bee keeping) or swarming.
- (5) The feedback mechanisms that work within the colony cause delayed disturbances of the age demography structure in response to disturbances of resource influx or in response to colony manipulations.
- (6) Disturbances of the age demography structure affect the division of labor, what in turn affects the resource status of the colony.

To investigate the implications of these assumptions, we created “HoPoMo”, a honeybee population model that allows us to investigate the effects over time of a decline in food influx, of bad weather periods, of a decline in the number of offspring, of other changes in demography, or of a loss of stored food resources in the honeybee collective. The model projects the intracolony population dynamics of a colony, as well as its food management patterns and the allocation of adult bees to three important tasks: brood nursing, food collection and food processing. Concerning the food processing and allocation, we focused on the importance of pollen derived proteins and the impacts of possible protein stress on the demographic status of the colony (e.g., via cannibalism). The importance of pollen insufficiency and bad weather periods for real honeybee colonies is described in [Dustmann and von der Ohe \(1988\)](#). Demographic changes lead to disturbances in the usually well-balanced division of labor and in the homeostatic resource allocation, what in turn can influence the age demography again. The model presented here is the very first mathematical model that considers this important aspects of honeybee population dynamics, as was investigated empirically ([Schmickl and Crailsheim, 2001, 2002](#); [Schmickl et al., 2003](#)) and reviewed ([Schmickl and Crailsheim, 2004a](#)) by the authors.

Within this article, we first formulate the model and explain how its equations were derived from published empirical findings. We offer a basic framework for building onto the foundation given here. This is why we explicitly describe all equations, all parameter values and all constraints of our model in this article. In the second part of this article, we perform a validity check that compares simulation results with empirical data. In a third step, we analyze the global sensitivity of the model and the sensitivity to single parameter changes. We also check the correct “flow of mass” within this section. The fourth part of the article demonstrates how the model can be used to investigate special conditions of bee keeping by the example of a honeybee colony that is kept in a scientific observation hive. Finally, we demonstrate that the basic framework of the model can be easily extended to treat also wild-life bees by simulating a colony that builds its comb from scratch into a cavity like in a hollow tree and that divides by swarming and is exposed to real weather data.

2. Model implementation

This is an age structured population model that tracks several cohorts of bees of distinct ages. The model works with discrete time steps, each 1 day wide, using difference equations. This approach was used in population models of another social insect species: *Vespa simillima* ([Martin, 1991](#)). Also [Harris \(1995\)](#), who modeled a honeybee population in discrete age classes, inspired our approach. The model is implemented in Mathematica® by defining functions and retrieving values in discrete steps representing each day of year starting on the 1st of January. For readers who are not familiar with the Mathematica® formula syntax, we use standard mathematical expressions in this article.

2.1. Modeling the queen's egg laying behavior

[Omholt \(1986, 1992\)](#) modeled the daily egg laying of the queen in dependence of the adult worker population in the hive. [Makela et al. \(1993\)](#) also modeled this relationship, but added also day-length and resource influx as factors that influence the daily egg laying of the queen. [DeGrandi-Hoffman et al. \(1989\)](#) used additionally the ambient temperature to modulate the egg laying of the queen in their model.

It is obvious that the size of the adult bee population at the time of maximum egg laying is significantly bigger compared to the overwintering population and that the egg laying rate decreases after this moment. But it is not clear, whether there is a causal dependency of the down-modulation of the egg laying rate on the adult population size or there is simply a coincidence of these two facts. Undoubtedly, the availability of resources, the day-length and the average ambient temperature corresponds strongly to the season and to the climate region, as do the egg laying patterns of honeybee queens. For keeping our model as stable and as simple as possible, we combined all these factors into one “seasonal profile” called season(t) in our model. By manipulating season(t), the user can adopt the model to different climate regions.

We defined season(t) (the “seasonal factor”) as a function of day number t. In our model, this factor not only influences the daily egg laying rate of the queen, it also affects nectar and pollen availability in the environment. [Fig. 1a](#) shows the values of season(t) throughout a full year. By adjusting the values of the five parameters x_1 , x_2 , x_3 , x_4 , and x_5 , the shape of the seasonal factor season(t) can be adjusted to different climate zones. For example, the parameter x_4 determines the day of the year, where the modeled queen shows the maximum egg laying activity.

$$\text{season}(t) = \max \left\{ \begin{array}{l} 1 - \frac{1}{1 + x_1 e^{-2t/x_2}} \\ \frac{1}{1 + x_3 e^{-2(t-x_4)/x_5}} \end{array} \right. \quad (1)$$

Our model also includes a second component that influences the queen's egg laying activity: spatial factors inside the hive. Some other factors, such as the special egg laying dynamics in the pre- and post-swarming periods, are omitted in the model presented here. In some of our recent experiments that used three-frame observation hives, we noticed a cessation of the queens egg laying activity in times when the available brood nest area was restricted (data not shown). This cessation lasted until new bees emerge and their cells are prepared for re-use. To incorporate this fact into our model, we introduced a factor called SUPcomb(t), which describes the suppression in egg laying when the available empty space in the hive is below a threshold value of the parameter SUPthreshold. We interpret this gradual lowering of the queen's egg laying as being caused by an increased searching time for suitable empty cells. To calculate the ratio of available empty cells to total cells, we defined the constant CELLShive as the total number of cells in the hive.

Our basic model does not include the task “comb building”. In the last ecological scenario modelled in this article (see [Section 4.6](#)), we depict the population dynamics of a wild hon-

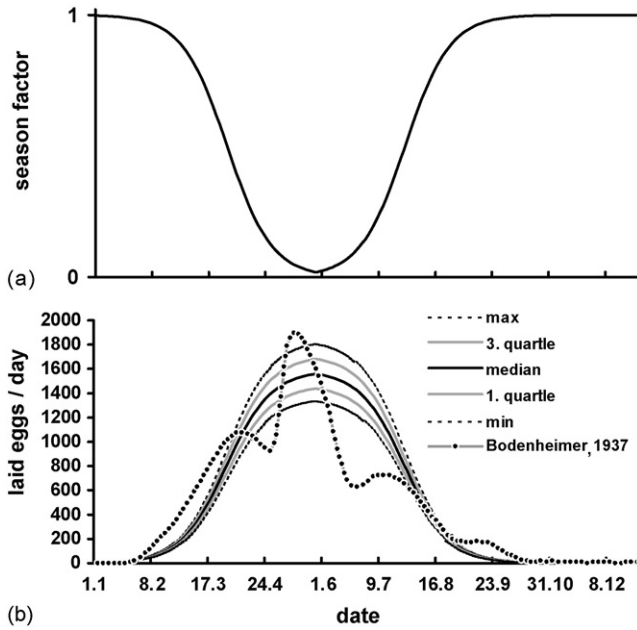


Fig. 1 – (a) The dynamics of the “seasonal factor” parameter (season(t)) throughout a year. This factor is defined in Eq. (1) and is used for modeling seasonal influence on the queen’s egg laying and on environmental food supply. (b) The daily egg laying activity (ELR(t), defined in Eq. (5)) of the honeybee queen in our model (median, maximum, minimum and quartiles of 1000 simulation runs; all parameters varied within a range of $\pm 15\%$). Literature data redrawn from Bodenheimer (1937) is presented to allow comparison with empirical data.

eybee swarm. This swarm has to build its combs from scratch what was implemented by exchanging the constant CELLShive by a function of time CELLShive(t).

$$\text{CELLSempty}(t) = \text{CELLShive} - \text{CELLSbrood}(t) - \text{STORESpollen}(t) - \text{STORESnectar}(t) - \text{STOREShoney}(t) \quad (2)$$

$$\text{SUPcomb}(t) = \begin{cases} \frac{\text{CELLSempty}(t)}{(\text{CELLShive} + 1) \cdot \text{SUPthreshold}}, & \text{if } \frac{\text{CELLSempty}(t)}{\text{CELLShive} + 1} < \text{SUPthreshold} \\ 1, & \text{else} \end{cases} \quad (3)$$

As the queen shows a high variability in egg laying activity even in situations with enough empty cells available (personal observation), we apply an additional, stochastic factor, ELRstoch(t). This stochastic factor can be set to zero (no fluctuations) if preferred in simulations. We assume this stochastic value to be uniformly distributed around zero and to vary between $-\text{ELRstochrange}$ and $+\text{ELRstochrange}$.

$$\text{ELRstoch}(t) = \text{Random}(\text{Real}, -\text{ELRstochrange}, +\text{ELRstochrange}) \quad (4)$$

Using the factors mentioned above, we model the overall daily egg laying rate as follows:

$$\text{ELR}(t) = \text{ELRbase} \cdot (1 + \text{ELRstoch}(t)) \cdot (1 - \text{season}(t)) \cdot \text{SUPcomb}(t) \quad (5)$$

ELR(t) is the predicted egg laying rate of the queen on day t. The parameter ELRbase is the mean daily egg laying rate of the queen at the maximum egg laying peak in spring (in temperate regions). Queens differ individually in this maximum egg laying capacity, thus ELRbase represents a genetic component. This parameter can also be used to model the age of the honeybee queen, because the maximum egg laying rate of a queen depends also on the queen’s age.

2.2. Modeling the immature stages

The published values for the durations of the developmental stages “egg”, “larva”, and “sealed brood” (=“prepupa” and “pupa”) are not consistent in the literature. We model the brood in discrete stages lasting 3 days, 5 days and 12 days, respectively, following the suggestions of Garofalo (1977). These developmental periods are implemented using the constants LIFESPANegg, LIFESPANlarvae, LIFESPANpupa. We use a set of two-dimensional variables EGGS(i, t), LARVAE(i, t), and PUPAE(i, t) to model the amount of brood on each day t, where i indicates the age of the immature individual, in days. The initial population state of the colony on day $t=0$ is given by the variables EGGS(i, 0), LARVAE(i, 0), PUPAE(i, 0). We model the aging of each age cohort into the next age class in discrete steps of 1 day: all surviving individuals of an age cohort are shifted into the next age class on the next day. For example, $\text{LARVAE}[i, t] = \text{LARVAE}[i - 1, t - 1]$, if we assume zero mortality. To account for the significant loss of immature bees, we introduced several mortality factors for immature stages into our model.

2.2.1. Eggs

We found a quite constant daily egg mortality (MORTALITYeggs) in our recent experiments (unpublished data). This “disappearing” of eggs at a certain rate has been described

by Myser (1952) and Merill (1924). The number of 1-day-old eggs is derived from the egg laying rate on the previous day ($\text{ELR}(t - 1)$). The number of 2- or 3-day-old eggs is derived from the number of eggs 1 day younger on the previous day ($\text{EGGS}(i - 1, t - 1)$):

$$\text{EGGS}(i, t) = \begin{cases} \text{ELR}(t - 1)(1 - \text{MORTALITYeggs}), & \text{if } i = 1 \\ \text{EGGS}(i - 1, t - 1)(1 - \text{MORTALITYeggs}), & \text{if } i \in \{2, 3\} \end{cases} \quad (6)$$

Based on Eq. (6) we can calculate the daily total number of eggs as follows:

$$\text{CELLSeggs}(t) = \sum_{i=1}^{\text{LIFESPANegg}} (\text{EGGS}(i, t)) \quad (7)$$

$$\text{LARVAE}(i, t) = \begin{cases} \text{EGGS}(\text{LIFESPANegg}, t - 1) \cdot \text{SURVIVALlarvae}(1, t), & \text{if } i = 1 \\ \text{LARVAE}(i - 1, t - 1) \cdot \text{SURVIVALlarvae}(i, t), & \text{if } 1 < i \leq \text{LIFESPANlarva} \end{cases} \quad (11)$$

Alternatively, we can calculate $\text{CELLSeggs}(t)$ more directly as follows:

$$\text{CELLSeggs}(t) = \sum_{i=1}^{\text{LIFESPANegg}} (\text{ELR}(t - i)(1 - \text{MORTALITYeggs})^i) \quad (8)$$

$$\text{CELLSlarvae}(t) = \sum_{i=1}^{\text{LIFESPANlarva}} \left(\text{ELR}(t - i - \text{LIFESPANegg}) \cdot (1 - \text{MORTALITYeggs})^{\text{LIFESPANegg}} \cdot \left(\prod_{k=1}^i \text{SURVIVALlarvae}(k, t - i + k) \right) \right) \quad (13)$$

2.2.2. Larvae (unsealed)

Concerning larvae, we modeled the aging process almost the same way as we did it with eggs, except that larval mortality is more complex. Larvae are frequently cannibalized in a honeybee colony, and the rate of cannibalism depends on the age of the larvae (Schmickl and Crailsheim, 2001), the

$$\text{PUPAE}(i, t) = \begin{cases} \text{LARVAE}(\text{LIFESPANlarva}, t - 1) \cdot (1 - \text{MORTALITYpupae}), & \text{if } i = 1 \\ \text{PUPAE}(i - 1, t - 1) \cdot (1 - \text{MORTALITYpupae}), & \text{if } 1 < i \leq \text{LIFESPANpupa} \end{cases} \quad (14)$$

pollen status of the colony (Schmickl and Crailsheim, 2001) and the ratio of workers to larvae (Eischen et al., 1982). We used a time-independent base mortality rate MORTALITYlarvae and another mortality factor $\text{CANNIBALISMlarvae}(i, t)$ that varies with the pollen status of the colony, the size of the nursing workforce, the larval age (i), and an age-specific basic cannibalism rate ($\text{CANNIBALISMhungerbase}(i)$). The changes in the pollen supply of the colony are expressed by $\text{INDEXpollensituation}(t)$, while changes in the colony's nursing capacity are expressed by $\text{INDEXnursingquality}(t)$. Allen and Jeffree (1956) showed that brood rearing is correlated with colony size (thus correlated with nursing workforce) and with the amount of pollen stores.

$$\text{SURVIVALlarvae}(i, t) = (1 - \text{CANNIBALISMlarvae}(i, t)) \cdot (1 - \text{MORTALITYlarvae}) \quad (9)$$

$$\text{CELLSpupae}(t) = \sum_{i=1}^{\text{LIFESPANpupa}} \left(\text{ELR}(t - i - \text{LIFESPANegg} - \text{LIFESPANlarva}) \cdot (1 - \text{MORTALITYeggs})^{\text{LIFESPANegg}} \cdot \left(\prod_{k=1}^{\text{LIFESPANlarva}} \text{SURVIVALlarvae}(k, t - i - \text{LIFESPANlarva} + k) \right) \cdot (1 - \text{MORTALITYpupae})^i \right) \quad (16)$$

$$\begin{aligned} \text{CANNIBALISMlarvae}(i, t) &= \text{CANNIBALISMhungerbase}(i) \\ &\cdot (1 - (\text{INDEXpollensituation}(t - 1) \\ &\cdot \text{INDEXnursingquality}(t - 1))) \end{aligned} \quad (10)$$

Now we can calculate the daily larval age demography by shifting the cohorts of larvae daily into the next age class and by reducing the numbers according to the calculated mortality rates.

From this age demography of larvae, we can calculate the daily number of cells that contain any age of unsealed larvae, either by summing $\text{LARVAE}(i, t)$ (Eq. (12)) or by directly calculating from the egg laying rates of the past days (Eq. (13)):

$$\text{CELLSlarvae}(t) = \sum_{i=1}^{\text{LIFESPANlarva}} \text{LARVAE}(i, t) \quad (12)$$

2.2.3. Pupae (sealed brood)

Compared to the larval population, the daily number of pupae is easier to calculate, as the mortality rate for sealed brood (MORTALITYpupae) is very low and almost constant (see Fukuda and Sakagami, 1968 for details).

We calculate the age demography of all sealed brood in the variable $\text{PUPAE}(i, t)$, neglecting the fact that on the first day after sealing of the cell, the brood is in the prepupa stage or even in the last larval stage. These cells are sealed, and the brood in it does not require any feedings by nurse bees, so it is “functionally” similar to pupae in our model.

Again, we can calculate the daily age demography of sealed brood by summing the variable defined in Eq. (14) (see Eq. (15)) or by calculating directly from the past egg laying of the queen (Eq. (16)).

$$\text{CELLSpupae}(t) = \sum_{i=1}^{\text{LIFESPANpupa}} \text{PUPAE}(i, t) \quad (15)$$

The total number of cells filled with brood can now be calculated as follows:

$$\begin{aligned} \text{CELLSbrood}(t) &= \text{CELLSeggs}(t) + \text{CELLSlarvae}(t) \\ &+ \text{CELLSpupae}(t) \end{aligned} \quad (17)$$

2.3. Modeling the population of adult bees

In our model, the number of adult bees is determined by two factors: the number of bees that hatch each day from the last

pupal stage and the number of bees that die each day. We use a constant basic adult mortality rate and a set of variable task-specific mortality rates for calculating those losses of adult bees.

In our model, the overall daily mortality rate of adult bees ($MORTALITY_{adult}(t)$) is composed of the basic constant mortality rate ($MORTALITY_{adultbase}$), the mortality rates for nursing bees ($MORTALITY_{nursing}$), the mortality rate for nectar processing bees ($MORTALITY_{processing}$) and the mortality rate of foraging bees ($MORTALITY_{foraging}$). Obviously, we used distinct mortality rates only for those tasks that are treated in our model. The task-specific mortality rates are weighted according to the daily ratio of bees performing the task to the total number of adult bees on that day.

$$\begin{aligned}
 MORTALITY_{adult}(t) &= MORTALITY_{adultbase} + MORTALITY_{nursing} \\
 &\quad \cdot \frac{NURSES(t-1)}{BEES_{adult}(t-1) + 1} + MORTALITY_{processing} \\
 &\quad \cdot \frac{PROCESSORS(t-1)}{BEES_{adult}(t-1) + 1} + MORTALITY_{foraging} \\
 &\quad \cdot \frac{FORAGERS_{active}(t-1)}{BEES_{adult}(t-1) + 1} \quad (18)
 \end{aligned}$$

We used the numbers of bees on the previous day ($t-1$) in Eq. (18) to prevent a circular formula definition with Eq. (19). Please note that although $MORTALITY_{foraging}$ is a constant factor, the influence of environmental conditions onto forager mortality is present in our model. Environmental conditions (temperature, rain and environmental resource availability) as well as the internal status of the colony (demand, foraging workforce, processing workforce) affect the size of $FORAGERS_{active}(t)$ and thus affect automatically the fraction of foraging-caused mortality within the overall adult mortality.

Knowing the overall mortality rate and the daily number of newly emerging bees, we can calculate the daily number of adult bees in the colony:

$$\begin{aligned}
 BEES_{adult}(t) &= (BEES_{adult}(t-1) + PUPAE(LIFESPAN_{pupa}, t-1)) \\
 &\quad \cdot (1 - MORTALITY_{adult}(t)) \quad (19)
 \end{aligned}$$

Although we model the working cohorts of nurse bees, processor bees and forager bees in Eqs. (29), (31) and (51), the only model variable that ensures “conservation of mass” is $BEES_{adult}(t)$. The cohorts of worker bees are assigned day by day as fractions of $BEES_{adult}(t)$. This is the reason why we have to compile all adult mortality rates into one daily factor (as a weighted average; see Eq. (18)) and then apply this weighted mortality factor to $BEES_{adult}(t)$ in Eq. (19).

2.4. Modeling the influence of the environment

One focus of our model is to allow projections of the effects of the environmental situation onto the development of the

colony. We use several indices that express aspects of the current outside environmental situation. The time-dependent parameter $INDEX_{rain}(t)$ has a value between 0 and 1. A value of 1 means that no rain affected the colony's foraging activity on day t , while a value of 0 means that continuous heavy rain prevented all foraging on that day. A value in between means that the bees were prevented from foraging for some fraction of the day (e.g., $INDEX_{rain}(t) = 0.5$ means foraging for one-half of the day). When we used these indices for feeding our model with real data in simulation runs, we took weather data that were recorded hourly and we calculated the average rain value during the daylight hours typically available for foraging flights. Using the parameter $RAIN(t)$, which expresses the rainy hours as a fraction of all daylight hours per day:

$$INDEX_{rain}(t) = 1 - RAIN(t) \quad (20)$$

$$RAIN(t) = \frac{HOURS_{raining\ during\ daylight}(t)}{HOURS_{daylight}(t)} \quad (21)$$

The parameter $INDEX_{temperature}(t)$ models the influence of outside temperature on the bees' flight activity. Bees tend to cease flight activity when it is too cold or too warm. We assume no flights below 14 °C, a linear increase of flight activity between 14 and 22 °C, optimal flight conditions between 22 and 32 °C and a linear decrease in flight activity between 32 and 40 °C. Above 40 °C (daytime mean value!), we assume no flight activity. A value of $INDEX_{temperature}(t) = 1$ means that temperature allows full flight activity, while a value of $INDEX_{temperature}(t) = 0$ means that all flights cease due to outside temperature. $TEMP(t)$ is the mean daily temperature calculated for the time window between 8:00 a.m. and 10:00 p.m. The influence of weather on the flight activity of honey-bee colonies is described in Szabo (1980), who showed the dependence of flight activity (and of colony weight gain) on temperature: below 14 °C, the bees in the observed colonies did not show flight activity. Between 14 and 22 °C, the bees in the observed colonies showed an almost linear increase in flight activity.

$$INDEX_{temperature}(t) = \begin{cases} 0, & \text{if } TEMP(t) \leq 14 \\ \frac{TEMP(t) - 14}{8}, & \text{if } 14 < TEMP(t) \leq 22 \\ 1, & \text{if } 22 < TEMP(t) \leq 32 \\ \frac{40 - TEMP(t)}{8}, & \text{if } 32 < TEMP(t) \leq 40 \\ 0, & \text{if } TEMP(t) > 40 \end{cases} \quad (22)$$

Combining these environmental factors, we calculate an index that expresses the overall flight weather quality as a number between 0 and 1 called $INDEX_{flight}(t)$. A value of 1 means perfect flight conditions for bees, a value of 0 means the worst flight conditions for bees.

$$INDEX_{flight}(t) = INDEX_{rain}(t) \cdot INDEX_{temperature}(t) \quad (23)$$

Additional indices express the environmental (botanical) supply of nectar and pollen, both of which also affect the ratio

of successful foraging flights to the total number of flights. Lacking concrete empirical data on botanical resource supply, we used the “seasonal factor” described in Eq. (1) to model these two variables:

$$\text{INDEXnectaroutside}(t) = \min \begin{cases} (1 - \text{season}(t)) \cdot 1.5 \\ 1 \end{cases} \quad (24)$$

$$\text{INDEXpollenoutside}(t) = \min \begin{cases} (1 - \text{season}(t)) \cdot 1.5 \\ 1 \end{cases} \quad (25)$$

By multiplying $(1 - \text{season}(t))$ by 1.5 we achieve maximum food availability ($\text{INDEXnectaroutside} = \text{INDEXpollenoutside} = 1$) from the first week of April to the end of July. Beginning in August, food availability in the environment diminishes day by day; it takes until the first week of September to fall below the 10% mark.

2.5. Modeling task decisions

The number of adult worker bees that are projected by the model for each day of the year represents the total workforce of the colony. This workforce is distributed among several cohorts of bees which perform tasks characteristic of their ages: nursing of brood, foraging and processing of food. The cohort of foragers is subdivided into foragers that collect pollen and foragers that collect nectar. We omitted the tasks of foraging for water and foraging for propolis in our model. Our model assumes that there are two tasks of such high priority that an inadequate workforce performing either one could significantly disturb the colony's working structure. The first is the task of brood nursing. The brood steadily consumes nutrients and must be constantly fed by nurse bees (Haydak, 1963a); otherwise the brood will die, which would cause severe damage to the colony's age structure (Dustmann and von der Ohe, 1988). The second key task is the collection of pollen. Pollen is stored only in small quantities, so that there is only a very short reserve. Fresh pollen (see Haydak, 1963b) is important for brood nursing (Allen and Jeffree, 1956; Webster et al., 1985).

In our model we first calculate the total workload for nursing and for pollen foraging on each day. If the available workforce (adult bees) is large enough, we assign enough workers to fully handle these two tasks. The remaining bees, if any (those, who are not nursing and are not foraging for pollen), are treated as being potentially involved in the nectar-connected tasks. We model the daily worker need in the two high-priority tasks ($\text{NEEDworkers}(t)$) as follows:

$$\text{NEEDworkers}(t) = \text{NEEDnurses}(t) + \text{NEEDpollenforagers}(t) \quad (26)$$

In times of low adult population and high working demand, it can happen that the workload is higher than the actual workforce. In these times, high-priority work can only be partially completed and the full number of needed working bees cannot be supplied. In this situation, our model allocates the workforce among the two high-priority tasks (nursing and pollen foraging). We calculate the daily ratio of workforce to

workload ($\text{RATIOworkforce}(t)$) as follows:

$$\text{RATIOworkforce}(t) = \min \begin{cases} \frac{\text{BEESadult}(t) \cdot (1 - \text{FACTORothertasks})}{\text{NEEDworkers}(t) + 1} \\ 1 \end{cases} \quad (27)$$

If $\text{RATIOworkforce}(t) < 1$, then the fraction $(1 - \text{RATIOworkforce}(t))$ of the needed work could not be completed on day t . The parameter FACTORothertasks accounts for the fraction of the adult bee population engaged in tasks that are not associated with the modeled task-groups: guarding, defense, cleaning, undertaking, wax-manipulation, comb-construction, scouting, care for the queen, etc. In our simulation, $\text{FACTORothertasks} = 0.2$.

2.6. Modeling the regulation of nursing

As described above, brood nursing is probably the most important task. A few days of poorly fed larvae leads to the production of adult bees that, when they attain nurse bee age, have a lowered ability to nurse brood. This results in a repeated, delayed negative feedback effect for the whole colony (Dustmann and von der Ohe, 1988). In contrast, even several days of no nectar foraging does not reduce the amount of nectar stores dramatically (Blaschon et al., 1999). Several studies (Stabe, 1930; Wang, 1965) have shown that unsealed brood grow in mass almost exponentially within the first 5 days of the larval stage, which coincides with an almost exponential growth in the nursing they receive from nursing bees (Lindauer, 1952). From that information we conclude that the nursing workload for larvae is dependent on larval age. We modeled ($\text{NEEDnurse_per_larva}(i)$) in 1-day-wide age classes. $\text{NEEDnurses_per_pupa}$ and $\text{NEEDnurses_per_egg}$ are modelled with smaller, age-independent values, as the developmental stages “egg” and “pupa” do not require feedings and do not grow in mass. The variable $\text{NEEDnurses}(t)$ sums up the total nursing demand of all brood stages.

$$\begin{aligned} \text{NEEDnurses}(t) &= \left(\sum_{i=1}^{\text{LIFESPANlarva}} (\text{LARVAE}(i, t) \cdot \text{NEEDnurses_per_larva}(i)) \right) \\ &+ \text{CELLSeggs}(t) \cdot \text{NEEDnurses_per_egg} + \text{CELLSpupae}(t) \\ &\cdot \text{NEEDnurses_per_pupa} \end{aligned} \quad (28)$$

$$\text{NURSES}(t) = \text{NEEDnurses}(t) \cdot \text{RATIOworkforce}(t) \quad (29)$$

$$\text{INDEXnursingquality}(t) = \frac{\text{NURSES}(t)}{\text{NEEDnurses}(t) + 1} \quad (30)$$

The variable $\text{NURSES}(t)$ represents the number of active nursing bees, taking into consideration that the larval need is not fully met if the value of $\text{RATIOworkforce}(t)$ is below 1. In that case, the value of $\text{INDEXnursingquality}(t)$ is also below 1. This index is used for modeling an important feedback loop, as it influences the brood mortality in Eq. (10). Please note that

in nature there can be qualitative differences between nursing bees, e.g., a low nurse-to-larva ratio can lead to the production of adult bees that work less efficiently when they assume the role of nursing bees (Eischen et al., 1984). We did not account for this fact; in our model all nursing bees are equally effective.

2.7. Modeling the regulation of foraging

The variable FORAGERS(t) models the daily number of potential foragers as the sum of potential pollen foragers and potential nectar foragers. This does not mean that all potential foragers on day t actively fly out and forage on that day; FORAGERS(t) just represents the available workforce for the foraging task. The actual number of foragers that fly out is calculated by the variable FORAGERSactive(t) and is mainly influenced by the outside weather factors, as expressed by INDEXflight(t), as well as by the botanical factors INDEXnectaroutside(t) and INDEXpollenoutside(t).

$$\text{FORAGERS}(t) = \text{FORAGERSpollen}(t) + \text{FORAGERSnectar}(t) \quad (31)$$

$$\text{FORAGERSactive}(t) = \text{FORAGERSpollenactive}(t) + \text{FORAGERSnectaractive}(t) \quad (32)$$

2.7.1. Recruitment of pollen foragers

Studies have shown that pollen stores are regulated in a homeostatic way (reviewed in detail in Schmickl and Crailsheim, 2004a). The more pollen is currently needed by a colony, the more of its foragers forage for pollen. This was shown by experimental removal or addition of pollen as well as by experimental removal or addition of brood (Barker, 1971; Dreller et al., 1999; Fewell and Winston, 1992). As the main pollen consumers are nursing bees (Moritz and Crailsheim, 1987) and brood, pollen stores are correlated with the brood status of the colony (Wille et al., 1985). Hellmich and Rothenbuhler (1986a) showed that both pollen usage and pollen collection are correlated with the number of larvae in the colony. Pankiw et al. (1998) showed that pollen foraging activity can also be increased by adding brood pheromones instead of real brood, suggesting a pheromone-based regulatory mechanism, while Vaughan and Calderone (2002) suggest a contact-based system and Camazine (1993) and Camazine et al. (1998) suggest

$$\text{NEEDpollen}(t) = \text{NEEDpollen.larvae}(t) + \text{NEEDpollen.adult}(t) \quad (33)$$

The pollen demand of larvae of all ages (i) is calculated by summing the age-dependent parameter POLLENNEEDlarva(i). The adult's pollen demand is calculated by adding the basic daily pollen demand of adult bees (a constant, POLLENNEEDadult) and an additional daily pollen demand of nursing bees (a constant, POLLENNEEDnurse).

$$\text{NEEDpollen.larvae}(t) = \sum_{i=1}^{\text{LIFESPANlarva}} (\text{POLLENNEEDlarva}(i) \cdot \text{LARVAE}(i, t)) \quad (34)$$

$$\text{NEEDpollen.adult}(t) = \text{BEESadult}(t) \cdot \text{POLLENNEEDadult} + \text{NURSES}(t) \cdot \text{POLLENNEEDnurse} \quad (35)$$

Although honey bees collect pollen according to the current demand, they always have a small pollen reserve stored inside the hive. Blaschon et al. (1999) showed that after a few days of rain, which prevents the colony from foraging, the pollen stores have diminished. In our model, the constant FACTORpollenstorage sets this storage level. A value of FACTORpollenstorage=6 means that the modeled colony regulates the pollen stores around a level that represents a reserve for approximately 6 days, based on the current level of demand. We use a gliding average throughout 3 days to model the needed pollen income to achieve this homeostatic regulation to incorporate possible time delays in the associated feedback loops within real colonies.

Hellmich and Rothenbuhler (1986b) showed that different genetic lines of honey bees collected pollen in reserves at different levels, but all used the pollen at the same level: according to the amount of brood (and therefore the demand). So we assume that FACTORpollenstorage expresses these genetic difference and we use this factor in modeling pollen foraging but not in modeling the usage of pollen.

$$\text{NEEDpollenincome}(t) = \max \left\{ \frac{\sum_{d=0}^2 \text{NEEDpollen}(t-d)}{3} \cdot \text{FACTORpollenstorage} - \text{STORESpollen}(t), 0 \right\} \quad (36)$$

a feeding-based mechanism. Our model does not incorporate the informational pathway the regulatory system is based on, it only incorporates the fact that pollen foraging is regulated according to the current pollen demand.

We calculate the colony's pollen demand (NEEDpollen(t)) by taking into consideration the pollen demands of the larvae and the pollen demands of adult bees.

Knowing the daily need for pollen income, we can calculate the needed number of pollen foragers (NEEDpollenforagers(t)). To calculate this, we take into consideration the following parameters and variables: LOADpollenforager (the amount of pollen collected per foraging trip; expressed in the unit "cellfuls", according to Camazine et al., 1990) and TURNSpollenforager (the number of trips performed per forager per day).

$$\text{NEEDpollenforagers}(t) = \frac{\text{NEEDpollenincome}(t-1)}{\text{LOADpollenforager} \cdot \text{TURNSpollenforager} \cdot \text{FACTORforagingsuccess}} \quad (37)$$

Weidenmüller and Tautz (2002) showed, that in times of high pollen need, the colony responds with a high number of pollen foragers but does not change the overall flight activity or the total number of all foragers (pollen and nectar). In our model, the group of foragers (nectar and pollen) is limited by the constant $FACTOR_{foragingmax}$. Eq. (37) models the number of pollen foragers needed according to the current need for additional pollen. In our model, the recruitment of pollen foragers is performed preferentially (due to Eq. (26)) compared to the recruitment of nectar foragers. This automatically increases the ratio of pollen foragers to nectar foragers without automatically increasing the total number of foragers.

In nature, there is always a certain minimum number of pollen foragers within the cohort of foragers, even when there is almost no pollen need (personal observation). The constant parameter $FACTOR_{minpollenforagers}$ expresses this (assumedly genetic) predisposition of some bees for pollen foraging.

$$FORAGERS_{pollen}(t) = \min \left\{ \begin{array}{l} \max \left\{ \begin{array}{l} NEED_{pollenforagers}(t) \cdot RATIO_{workforce}(t) \\ (BEES_{adult}(t) - NURSES(t)) \cdot FACTOR_{minpollenforagers} \end{array} \right. \\ BEES_{adult}(t) \cdot FACTOR_{foragingmax} \end{array} \right. \quad (38)$$

$$\begin{aligned} FORAGERS_{pollenactive}(t) \\ = FORAGER_{pollen}(t) \cdot INDEX_{flight}(t) \\ \cdot INDEX_{pollenoutside}(t) \end{aligned} \quad (39)$$

$$WORKFORCE_{nectar}(t) = \begin{cases} (BEES_{adult}(t) \cdot (1 - FACTOR_{othertasks})) - NURSES(t) - FORAGERS_{pollen}(t), & \text{if } RATIO_{workforce}(t) = 1 \\ 0, & \text{else} \end{cases} \quad (43)$$

$$FORAGERS_{nectar}(t) = \min \left\{ \begin{array}{l} (BEES_{adult}(t) \cdot FACTOR_{foragingmax}) - FORAGERS_{pollen}(t) \\ WORKFORCE_{nectar}(t) - PROCESSORS(t) \end{array} \right. \quad (44)$$

The variable $FORAGERS_{pollen}(t)$ models the potential number of pollen foragers each day. The number of foragers that actually leave the hive for foraging flights depends on two environmental factors: $INDEX_{flight}(t)$ expresses the weather situation each day, $INDEX_{pollenoutside}(t)$ expresses the botanical pollen availability each day. Only if the weather (rain, temperature) allows foraging flights and only if pollen sources are available will there be mass recruitment via bee dances, leading to significant foraging activity.

2.7.2. Recruitment of nectar foragers

We model the demand for nectar quite similarly to the modeling of pollen demand, with the additional complication that the active foragers are also important nectar consumers (see Eq. (42)).

$$NEED_{nectar}(t) = NEED_{nectar_larvae}(t) + NEED_{nectar_adult}(t) \quad (40)$$

$$NEED_{nectar_larvae}(t) = \sum_{i=1}^{LIFESPAN_{larva}} (NECTAR_{NEED}_{larva}(i) \cdot LARVAE(i, t)) \quad (41)$$

$$\begin{aligned} NEED_{nectar_adult}(t) = & BEES_{adult}(t) \cdot NECTAR_{NEED}_{adult} \\ & + NURSES(t) \cdot NECTAR_{NEED}_{nurse} \\ & + FORAGES_{active}(t) \\ & \cdot NECTAR_{NEED}_{activeforager} \end{aligned} \quad (42)$$

In contrast to pollen collection, nectar collection is not regulated homeostatically. Nectar is collected in excess when

conditions permit. In our model, we recruit all available foraging bees, except those already recruited for collecting pollen, to tasks associated with the collection of nectar. Because the number of available workers could already be recruited for the high-priority jobs “nursing” and “pollen foraging” ($RATIO_{workforce} < 1$), it is necessary to limit $WORKFORCE_{nectar}(t)$ to non-negative values.

$$\begin{aligned} FORAGERS_{nectaractive}(t) \\ = FORAGERS_{nectar}(t) \cdot INDEX_{flight}(t) \\ \cdot INDEX_{nectaroutside}(t) \end{aligned} \quad (45)$$

$WORKFORCE_{nectar}(t)$ calculates the number of adult bees that are not involved in other tasks and thus are still available for a task associated with nectar collection. $FORAGERS_{nectar}(t)$ models the number of potential nectar foragers, taking into consideration that a fraction of $WORKFORCE_{nectar}(t)$ is already associated with the nectar processing task. But only when flight weather is good ($INDEX_{flight}(t)$ is near 1) and when environmental nectar supply is high ($INDEX_{nectaroutside}(t)$ is near 1), will many bees be recruited to forage for nectar. The process of mass recruitment of bees to food sources via dances is described in detail in Frisch (1927), in Seeley (1994, 1989) and in Seeley et al. (1991).

2.8. Modeling the resource influx into the colony

At this point, the model “knows” the number of active pollen foragers and the number of active nectar foragers. Combining these variables with the number of foraging flights per forager per day and with the average load size, the model can project the daily influx of pollen and nectar as follows:

INCOMENectar(t)

$$= \min \begin{cases} \text{FORAGERSnectaractive}(t) \cdot \text{LOADnectarforager} \cdot \text{TURNStectarforager} \cdot \text{FACTORforagingstoch}(t) \cdot \text{FACTORforagingsuccess} \\ \text{CELLSempty}(t - 1) \end{cases} \quad (49)$$

INCOMEpollent(t)

$$= \text{FORAGERSpollenactive}(t) \cdot \text{LOADpollenforager} \cdot \text{TURNSpollenforager} \cdot \text{FACTORforagingstoch}(t) \cdot \text{FACTORforagingsuccess} \quad (46)$$

$$\text{FACTORforagingstoch}(t) = \begin{cases} 1, & \text{without a stochastic factor} \\ \text{Random}(\text{Real}, 0.75, 1.25), & \text{with a stochastic factor of } \pm 0.25 \end{cases} \quad (47)$$

Several parameters are involved in this modeling of foraging income: $\text{LOADpollenforagers}$ defines the amount of pollen that is collected per foraging trip. $\text{TURNSpollenforager}$ defines the number of daily trips an average pollen forager performs. $\text{FACTORforagingstoch}(t)$ is a stochastic factor involved in this process. And finally, $\text{FACTORforagingsuccess}$ expresses the overall success rate of foraging trips. It is necessary to note the fact that $\text{FACTORforagingstoch}(t)$ and $\text{FACTORforagingsuccess}$ are significantly different factors. While $\text{FACTORforagingstoch}(t)$ is time-dependent and is used to vary the daily foraging success symmetrically around 1 (thus just introduces daily fluctuations that compensate in the long run), $\text{FACTORforagingsuccess}$ expresses the fact that foragers do not find all food sources they are recruited to.

INDEXpollensituation(t)

$$= \min \begin{cases} 1 \\ \frac{\text{STORESpollen}(t)}{\text{NEEDpollen}(t) \cdot \text{FACTORpollenstorage} + 1} \end{cases} \quad (48)$$

The index $\text{INDEXpollensituation}(t)$ describes the level of the pollen stores in relation to the demand situation of the colony. We use this index in Eq. (10), influencing the cannibalism of larvae, and in Eq. (50), influencing the consumption of pollen. As the brood cannibalism reduces pollen demand by reducing the number of larvae, this is a very important feedback loop in the overall regulation system of inner nest homeostasis.

In modeling nectar collection, we must treat another scenario: in small hives, nectar might fill up almost all of the food storage cells, so that no additional influx is possible. The

model applies this restriction only on the collection of nectar and not on the collection of pollen, because the daily amount of collected nectar is usually much greater than the amount of collected pollen. In our model, the amount of collected pollen is so much lower than the amount of collected nectar and the number of cells devoted to daily egg laying that it was sufficient to apply an empty-space-dependent regulation only on nectar collection and on egg laying.

The parameters LOADnectarforager , $\text{TURNStectarforager}$, $\text{FACTORforagingstoch}(t)$ and $\text{FACTORforagingsuccess}$ correspond to the parameters used in modeling the daily pollen income in Eq. (46).

2.9. Regulation of food processing

Food processing bees are recruited in order to process the collected nectar (as measured in $\text{STORESnectar}(t)$) into honey.

Normally, nectar processing and nectar collection are balanced via the queuing delays experienced by nectar foragers waiting for nectar receivers. Thus, an increase in the amount of collected nectar decreases the number of nectar foragers and increases the number of nectar processors (Seeley, 1992). This balancing is a continuous process that works within hours or even faster. We found that the following simplification is satisfactory: as returning nectar foragers deposit their nectar loads, the loads are added to the variable ($\text{STORESnectar}(t)$). Depending on the amount of stored nectar, which mainly consists of the nectar collected on the previous day ($t - 1$), we calculate the needed nectar processors ($\text{NEEDprocessors}(t)$) on day t . As nectar processing has a higher priority in task selection than nectar foraging (see Eq. (44)), a high amount of unprocessed nectar results in a reduced number of available nectar foragers. Also, it can happen that the available workforce is limited (as in Eq. (43)) and not all nectar can be processed.

$$\text{NEEDprocessors}(t) = \text{STORESnectar}(t - 1) \cdot \text{ProcessorsPerCell} \quad (50)$$

$$\text{PROCESSORS}(t) = \min \begin{cases} \text{NEEDprocessors}(t) \\ \text{WORKFORCEnectar}(t) \end{cases} \quad (51)$$

PROCESSEDnectar(t)

$$= \min \begin{cases} \text{STORESnectar}(t - 1) - \text{USAGEnectar}(t) \\ \frac{\text{PROCESSORS}(t)}{\text{ProcessorsPerCell}} \end{cases} \quad (52)$$

This regulation system is a simplification of the system that acts in nature. In nature the balancing between nectar processing and nectar foraging is based on the queuing delays encountered by returning nectar foragers, leading to a dynamic balancing of these two task groups within minutes or at least within hours. We simplified the balancing mechanism by restricting the number of nectar foragers based on the nectar collected on the previous day, because the model works in discrete time steps of 1 day. To model the nectar processing/nectar-collection balancing mechanism explicitly, one would need to model at a finer resolution (hours or minutes). This was done in a series of models that analyzed the properties of this balancing mechanism (Anderson and Ratnieks, 1999; Ratnieks and Anderson, 1999; Anderson, 1998; Seeley and Tovey, 1994).

2.10. Management of nutrient stores

The level of pollen, nectar, and honey stores is influenced by the balance between consumption (usage) and collection (influx). The daily usage (consumption) of pollen (USAGEpollen(t)) depends on the size of the available pollen stores and on the current pollen supply situation, as expressed by the index INDEXpollensituation(t). Studies have shown that in times of poor pollen supply, the bees save pollen by feeding less to the brood (Schmickl et al., 2003; Schmickl and Crailsheim, 2002). But the bees can only reduce their usual consumption rate by a certain fraction, so the maximum saved pollen is defined by the constant FACTORpollensavingmax, which can be interpreted as a physiological component of the modeled colony. Accordingly to Hellmich and Rothenbuhler (1986b), the usage of pollen is not different between genetic lines that differ in their pollen hoarding behavior.

$$\text{USAGEpollen}(t) = \min \left\{ \begin{array}{l} \text{STORESpollen}(t-1) \\ \text{NEEDpollen}(t-1) \cdot (1 - (\text{FACTORpollensavingmax} \cdot (1 - \text{INDEXpollensituation}(t-1)))) \end{array} \right. \quad (53)$$

The daily amount of stored pollen can be calculated as follows:

$$\text{STORESpollen}(t) = \text{STORESpollen}(t-1) + \text{INCOMEpollen}(t) - \text{USAGEpollen}(t) \quad (54)$$

Analogously to the management of pollen stores, we model the management of honey stores and nectar stores. We model the daily processing of nectar into honey, a process that concentrates the nectar and thereby reduces the volume (as defined by the constant RATIOnectar.to.honey). We assume that the bees first consume the available (fresh) nectar for gaining their daily energy, and, if this does not satisfy demand, they take the rest from the honey stores. Utilizing stored honey happens mainly during winter, during times of bad weather or during periods of low availability.

$$\text{USAGEnectar}(t) = \min \left\{ \begin{array}{l} \text{STORESnectar}(t-1) \\ \text{NEEDnectar}(t) \end{array} \right. \quad (55)$$

$$\text{USAGEhoney}(t) = \min \left\{ \begin{array}{l} \text{STOREShoney}(t-1) \\ (\text{NEEDnectar}(t) - \text{USAGEnectar}(t)) \cdot \text{RATIOnectar.to.honey} \end{array} \right. \quad (56)$$

Based on Eqs. (49), (52), (55) and (56), we can calculate the daily amount of nectar stores and honey stores as follows:

$$\begin{aligned} \text{STORESnectar}(t) &= \text{STORESnectar}(t-1) + \text{INCOMEnectar}(t) \\ &\quad - \text{USAGEnectar}(t) - \text{PROCESSEDNectar}(t) \end{aligned} \quad (57)$$

$$\begin{aligned} \text{STOREShoney}(t) &= \text{STOREShoney}(t-1) - \text{USAGEhoney}(t) \\ &\quad + (\text{PROCESSEDNectar}(t) \\ &\quad \cdot \text{RATIOnectar.to.honey}) \end{aligned} \quad (58)$$

Now that the model has values for all contents of the hive on each day, we can calculate the predicted weight of the whole colony. The factors w_{pollen} , w_{nectar} , w_{honey} represent the weight of one cell filled with the given resource, respectively. The factors w_{egg} , w_{pupa} and w_{adult} represent the weight of a bee in the given stage. The factor $w_{\text{larva}}(i)$ represent the weight of a larva in age i . The parameter w_{hivebase} represents the weight of the hive, $w_{\text{cellsbase}}$ represents the weight of one empty cell (wax only). Because all these weights are given in g and WEIGHTcolony(t) is expressed in kilogram, we divide the result by 1000.

$$\begin{aligned} \text{WEIGHTcolony}(t) &= \frac{1}{1000} \cdot \left(w_{\text{hivebase}} + w_{\text{cellsbase}} \cdot \text{CELLShive} \right. \\ &\quad + w_{\text{pollen}} \cdot \text{STORESpollen}(t) + w_{\text{nectar}} \cdot \text{STORESnectar}(t) \\ &\quad + w_{\text{honey}} \cdot \text{STOREShoney}(t) + w_{\text{egg}} \cdot \text{CELLSeggs}(t) \\ &\quad + w_{\text{pupa}} \cdot \text{CELLSpupae}(t) \\ &\quad + \sum_{i=1}^{\text{LIFESPANlarva}} (w_{\text{larva}}(i) \cdot \text{LARVAE}(i, t)) \\ &\quad \left. + w_{\text{adult}} \cdot \text{BEESadult}(t) \right) \end{aligned} \quad (59)$$

Finally, at least in times of bad weather, of low demand or of low numbers of empty storage cells, a certain fraction of bees is not recruited for any task in our model. We calculate

this group as follows:

$$\begin{aligned} \text{BEESlazy}(t) = & (\text{BEESadult}(t) \cdot (1 - \text{FACTORothertasks})) \\ & - \text{FORAGERSactive}(t) - \text{NURSES}(t) \\ & - \text{PROCESSORS}(t) \end{aligned} \quad (60)$$

3. Parameterization

The parameterization is at least as important as the equations that were used to construct a model. We used values derived from own experimental data or from published literature to parameterize our model.

[Bodenheimer \(1937\)](#) described the maximum egg laying rate of honey bee queens to be between 1000 and 2000 eggs per day. We set the value of ELRbase to 1600 eggs per day and set the peak of egg laying to the first week of June (see [Fig. 1b](#)). [Fig. 1b](#) compares the seasonal egg laying pattern of our model to literature data from [Bodenheimer \(1937\)](#). In our model we set $\text{SUPthreshold} = 0.2$, thus, when fewer than 20% of the cells are empty, the egg laying rate of the queen starts to decline due to longer searching periods for suitable cells. In our simulation runs presented in this article, we set the size of the hive (CELLShive) to a value of 250,000 cells, which approximately corresponds to a colony consisting of 30–40 frames. In the simulation runs presented in this article, we adjusted the seasonal factor $\text{season}(t)$ by setting the five parameters x_1, x_2, x_3, x_4 , and x_5 to the values $x_{1-5} = \{385, 30, 36, 155, 30\}$. These parameter values were found to fit best to literature data (see [Fig. 1](#)).

Based on the data given by [Fukuda and Sakagami \(1968\)](#), we modeled the duration of immature stages as follows: $\text{LIFESPANegg} = 3$, $\text{LIFESPANlarva} = 5$, $\text{LIFESPANpupa} = 12$. Although our model does not work with a fixed age-based schedule for tasks performed by adult bees, we used the following task schedule to calculate an individual's daily pollen demand, daily nectar demand and task-specific mortality: baby-bee and cleaning bee: 0–3 days of age; nursing bee: 4–13 days of age; food processor bee and other in-hive tasks: 14–21 days of age; foraging bee: rest of life, with a mean duration of 11 days. These assumptions are consistent with the data shown in [Sakagami \(1953\)](#).

[Wang \(1965\)](#) and [Stabe \(1930\)](#) reported quasi-exponential mass gain of honeybee worker larvae (data depicted in [Fig. 2a](#)). Based on this fact we set our parameters to a quasi-exponential increase of pollen need and nectar need as a larva grows older ([Fig. 2b](#)). [Lindauer \(1952\)](#) also reported a quasi-exponential increase in the total nursing time a larva receives as she grows older (redrawn in [Fig. 2c](#)). According to that, we assumed that the number of nursing bees needed per larva per day also increases quasi-exponentially as the larva gets older ([Fig. 2d](#)). [Eischen et al. \(1982\)](#) reported an optimal worker-to-larva ratio of 4:1 for effective brood raising. Assuming that the maximum fraction of nursing bees within the adult bee population is 50%, this gives a ratio of 2:1. Because [Eischen et al. \(1982\)](#) used mixed-aged brood our model uses a higher level for 5-day-old larvae (3 nursing bees per larva per day) and lower values for larvae younger than 5 days.

Based on the above life schedule data, we calculated the pollen and nectar consumed to rear one bee: on average, a bee in our model needs 142.14 mg of pollen and 163.50 mg of nectar to be raised to adulthood. These values are very close to the 145 mg of pollen reported by [Alfonsus \(1933\)](#) and to the 163 mg of nectar reported by [Harbo \(1993\)](#). The mortality rates associated with developmental stages or associated with performed tasks are depicted in [Fig. 2e](#): we generated a simulated life-table based on the mortality rates which we used in our model and compared the resulting survivorship curve with data given by [Sakagami and Fukuda \(1968\)](#). We used the following mortality rates for immature stages: $\text{MORTALITYeggs} = 0.03$; $\text{MORTALITYlarvae} = 0.01$, $\text{MORTALITYpupae} = 0.001$. These rates are also consistent with the data given in [Garofalo \(1977\)](#). Based on the data shown in [Schmickl and Crailsheim \(2001\)](#), we set the age-dependent cannibalism rates to $\text{CANNIBALISMhungerbase}(i \in \{1, 2, \dots, 5\}) = \{0.23, 0.3, 0.58, 0.06, 0\}$.

For adult bees, we used the following mortality rates: $\text{MORTALITYbase} = 0.01$, $\text{MORTALITYnursing} = 0.005$, $\text{MORTALITYprocessing} = 0.005$, $\text{MORTALITYforaging} = 0.035$. The resulting survivorship curve is similar to the life-tables given in [Sakagami and Fukuda \(1968\)](#) (see [Fig. 2e](#) for the comparison). For the most risky task, which is foraging, [Visscher and Dukas \(1997\)](#) reported a log-linear survivorship curve of type II; this supports our approach to apply a constant mortality rate per time unit for foragers.

The basic unit for modeling the food flows in foraging tasks is “cellfuls” (also used by [Camazine et al., 1990](#)). We converted data given in kilogram, gram, microgram, millilitre and microlitre into the unit “cellful”, assuming that one cell filled with honey represents approximately 500 mg of honey (or 360 μl honey) and that one cell filled with pollen represents approximately 230 mg of pollen ([Camazine et al., 1990](#) and our own measurements).

On average, one pollen foraging flight results in 15 mg of collected pollen ([Seeley, 1995](#)). The amount of nectar collected per flight can vary over a wide range: [Seeley \(1995\)](#) reports 30 mg/flight, while [Huang and Seeley \(2004\)](#) report 12.6 μl /flight in times of low natural influx and 17.0 μl /flight in times of high natural influx; [Omholt \(1992\)](#) reports 15 mg/flight. Based on these data, we set $\text{LOADpollenforager} = 0.06$ cellfuls and $\text{LOADnectarforager} = 0.04$ cellfuls. Following [Omholt \(1992\)](#), we set the mean number of nectar foraging trips to $\text{TURNStectarforager} = 15$. Because foraging for pollen takes longer, we set $\text{TURNSpollenforager} = 10$. $\text{FACTORforagingsuccess}$ was set to 0.8, to account for the fact that not all foragers find the food source they are recruited to ([Seeley, 1995](#)).

To account for the fact that only a certain fraction of bees is involved in foraging and that a small fraction of foragers preferentially forage for pollen, we defined the two constants $\text{FACTORminpollenforagers} = 0.01$, and $\text{FACTORforagingmax} = 0.33$. Lacking experimental data, we assumed that one cell of nectar can be processed and stored by two processing bees ($\text{ProcessorsPerCell} = 2$). Data given by [Blaschon et al. \(1999\)](#) depicting pollen stores during artificial rain periods suggested the following parameter settings: $\text{FACTORpollenstorage} = 6$, $\text{FACTORpollensavingmax} = 0.3$. According

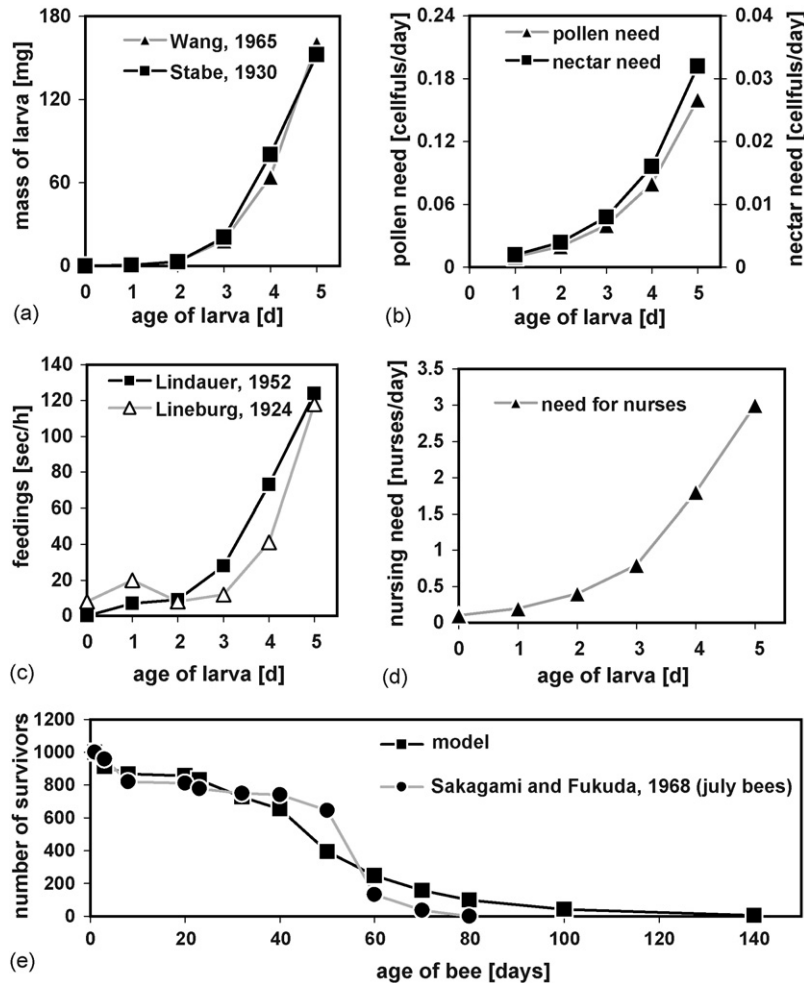


Fig. 2 – Empirical data from literature that were used to derive the important model parameters. (a) Mass gain of honeybee larvae redrawn from Wang (1965) and Stabe (1930). (b) Parametrization of the daily nectar demand and of the daily pollen demand of the larvae. (c) Feeding acts of differently aged larvae presented by Lindauer (1952) and Lineburg (1924), the unit “s/h” corresponds to “seconds of feeding per hour of observation”. (d) Daily demand for active nursing bees by differently aged larvae. (e) Comparison of a life table presented by Sakagami and Fukuda (1968) and our model’s simulated life table, demonstrating the effects of the mortality rates we used.

to data given in Seeley (1995), we set the $RATIO_{nectar_to_honey} = 20/50 = 0.4$.

For calculating the weight of the colony in Eq. (59), we used the following parameter values: $w_{cellbase} = 0.037$ g, $w_{pollen} = 0.23$ g, $w_{nectar} = 0.43$ g, $w_{honey} = 0.5$ g, $w_{egg} = 0.0001$ g, $w_{pupa} = 0.16$ g and $w_{adult} = 0.1$ g, $w_{larva}(i \in \{1, 2, \dots, 5\}) = \{0.0002$ g, 0.00059 g, 0.00331 g, 0.0644 g, 0.160 g}. The parameter $w_{hivebase}$ was set to 14,000 g (values are taken from Frisch, 1927; Stabe, 1930; Wang, 1965; Camazine et al., 1990).

4. Results of simulations

4.1. Validity check of the model

We performed 100 runs and varied all parameters within a range of $\pm 15\%$. Concerning the predicted total food consumption and food collection, our model compared very well to

empirical data: using the basic parameter setting (which was also used for the further analysis): 123,962 adult bees $\pm 10,731$ bees (mean $\pm$ S.D.) were produced throughout the year. These bees collected 19.26 ± 1.99 kg of pollen and 174.68 ± 23.96 kg of nectar. While the pollen was almost entirely consumed during the year, only 67.82 ± 6.78 kg of nectar was consumed. The remaining nectar was stored in the form of honey, having a weight of 49.65 ± 7.68 kg.

Seeley (1995) reports a brood production of 150,000 adult bees per year, an annual collection and consumption of approximately 20 kg of pollen, and an annual collection of 120 kg of nectar, of which approximately 70 kg are consumed. The remaining 50 kg of nectar are converted into 20 kg of honey. Except for the higher nectar total, our model projects these data very closely. While Seeley (1995) reports data from real colonies (facing unstable weather conditions) our simulation runs were performed under the assumptions of “optimal weather” and “optimal food availability” (see Eqs. (20)–(25); e.g., we set $Rain(t)$ to 0 for all $t \in \{0, 1, \dots, 365\}$).

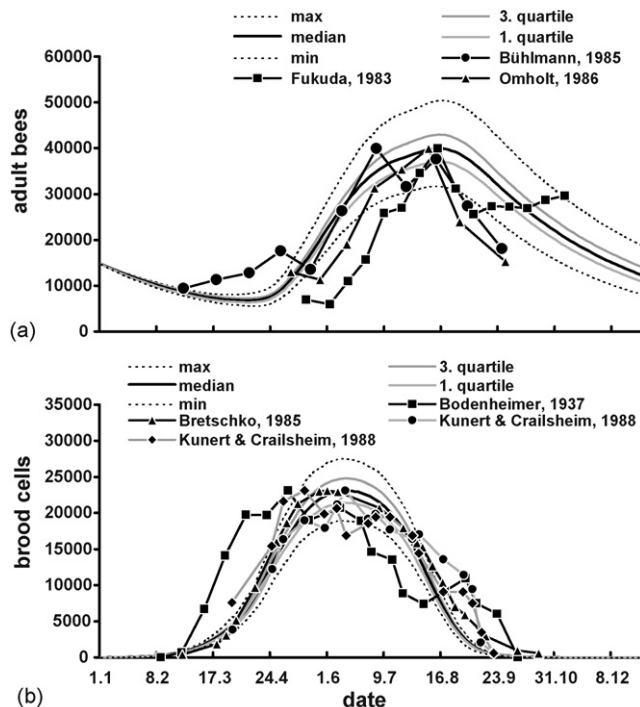


Fig. 3 – Intracolony population dynamics of adult bees (a) and brood cells (b) in our simulated honeybee colony throughout a year (median, maximum, minimum and quartiles of 1000 simulation runs; all parameters varied within a range of $\pm 15\%$). Empirical data from Bretschko (1995), Bühlmann (1985), Fukuda (1983), Omholt (1986), Bodenheimer (1937), and Kunert and Crailsheim (1988) are redrawn normalized to the maximum median value of the model to allow comparisons of the seasonal dynamics.

4.2. Sensitivity analysis of the model (changing all parameter values simultaneously)

We performed 1000 simulation runs and varied (with uniform random sampling) all input parameters within the range of $\pm 15\%$ (except LIFESPANegg, LIFESPANlarva, and LIFESPANpupa, because they have to be integer values, as our model works in discrete steps of $\Delta t = 1$ day). The constants LOADpollenforager, TURNSpollenforager and FACTORforagingsuccess were combined into one parameter in Eq. (46) in this analysis. The same was done with LOADnectarforager, TURNSnectarforager and FACTORforagingsuccess in Eq. (49).

Fig. 3a shows the dynamics of the adult bee population throughout the year. Our parameter variations of $\pm 15\%$ caused a variability of simulation runs between +26 (above the median run) and –21% (below the median run). In Fig. 3a, the timing of the population peak in mid-August is compared graphically to data given in Omholt, 1986, Fukuda (1983), and Bühlmann (1985). Because these studies were performed with different sizes of honeybee colonies, we normalized their data to the maximum level of our median model run. This way we did not influence the time dynamics of the literature data (the timing of the peak was not changed), we just re-scaled these data to allow better comparison of the time dynamics. The dynamics of the immature bee population in our simulation runs

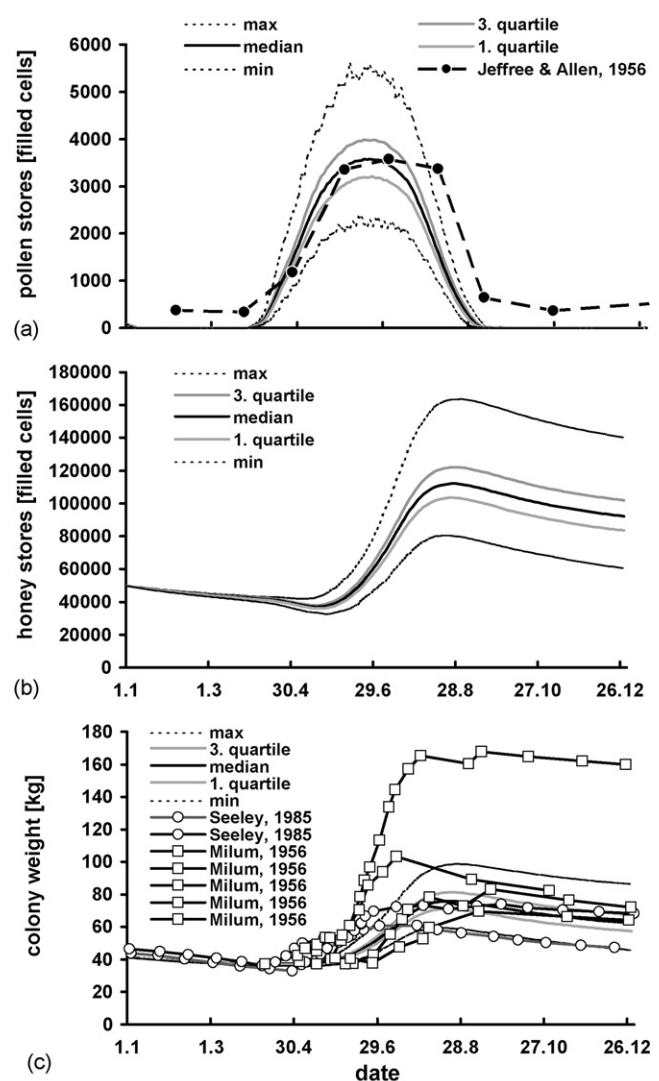


Fig. 4 – Seasonal dynamics of pollen stores (a) and honey stores (b) in our simulated honeybee colony throughout a year (median, maximum, minimum and quartiles of 1000 simulation runs; all parameters varied within a range of $\pm 15\%$). Empirical data from Jeffree and Allen (1956) are redrawn normalized to the maximum median value of the model to allow comparisons of the seasonal dynamics. (c) Projected colony weight of our simulated colony. Reference data were taken from Seeley (1985), who depicted the weight dynamics of a colony throughout the years 1981 and 1982, and from Milum (1956), who depicted 20 years of weight data of a honeybee colony; we selected the data from the years 1930, 1935, 1937, 1938 and 1955, because these years represent one “maximum”, one “minimum” and three “mid-range” runs. We assumed a base weight of the colony (hive and combs) of 15 kg. The model calculates daily weight by considering the number of adult bees and the brood population, as well as the level of nutritional stores (pollen, nectar, honey).

(=brood curve) is depicted in Fig. 3b. Our parameter variations ($\pm 15\%$) induced a variability of maximum brood population in simulation runs between +19 and -18% . Literature data (Bodenheimer, 1937; Bretschko, 1995; Kunert and Crailsheim, 1988) are depicted as reference points. Again, the literature data were normalized to the maximum brood level of the median simulation run.

Fig. 4a shows the seasonal pattern of pollen stores projected by our model. Our parameter variations ($\pm 15\%$) induced a variability between +56 and -34% for maximum pollen stores. Fig. 4a shows the data of Jeffree and Allen (1956) as reference points. We next consider the dynamics of honey stores. For maximum level of nectar stores, the variability of our results was within the span +46 to -28% . We found no published data on the development of honey stores (nobody seems to have measured the area of honey stores throughout a year). Several authors describe the changes in colony weight throughout the year (which is easy to measure) and point out that colony weight correlates with to the weight of the nectar and honey stores. However, because the brood and adult populations (and total weights) also change significantly throughout the year, we formulated Eq. (59) to calculate the daily weight of our modeled colony. Fig. 4c shows the weight development of our colony and compares it to literature data. The 15% variations in parameter settings led to a variability in colony weight results between +30 and -22% .

In a second analysis we kept the mortality rates and the base egg laying rate constant, to test the model's sensitivity to the foraging-related and task-related parameters. These parameters were again randomly sampled within a range of $\pm 15\%$, and 1000 simulation runs were performed. Fig. 5 depicts the results of these simulation runs. Compared to the data

given in Figs. 3 and 4, the span between minimum and maximum runs decreased markedly. In this analysis, the maximum adult population varied by $\pm 8\%$, while the maximum brood population varied between +4 and -6% . Pollen stores varied between +41 and -28% , while maximum honey stores varied between +35 and -26% .

Fig. 6 shows how the model deals with seasonal changes of environmental factors. In winter and early spring the usage of honey is considerably high. In summer, when there is a sufficient nectar influx, the usage of honey diminishes quickly, as the colony automatically switches to the consumption of the collected nectar.

In conclusion, the model's predictions on adult population, brood population, pollen stores and weight gain agree well with empirical honeybee data. These comparisons involved the total numbers per year as well as seasonal patterns (see Figs. 3 and 4). In addition, details of the resource allocation within the simulated colony (Fig. 6) reflect known empirical observations of honeybee colonies.

4.3. Sensitivity analysis of the model (changing one parameter only)

After testing the global sensitivity of our model, we inspected the model to determine which parameters it reacts most sensitively to. Thus, we varied one parameter between +40 and -40% of its standard value and measured the relative change in the following key criteria:

- K1: the adult population peak;
- K2: the brood population peak;
- K3: the maximum level of pollen stores (the pollen stores peak);

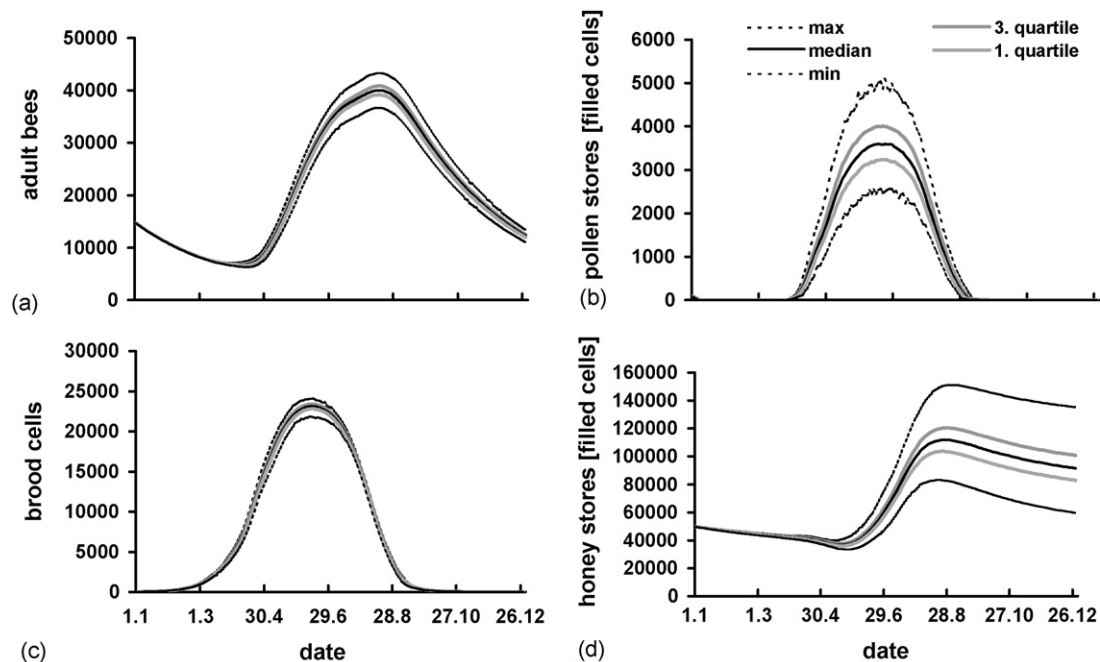


Fig. 5 – Population dynamics of adult bees (a), pollen stores (b), brood population (c) and honey stores (d) of a simulated honeybee colony throughout a year (median, maximum, minimum and quartiles of 1000 simulation runs; all parameters except mortality rates and egg laying rate were varied within a range of $\pm 15\%$).

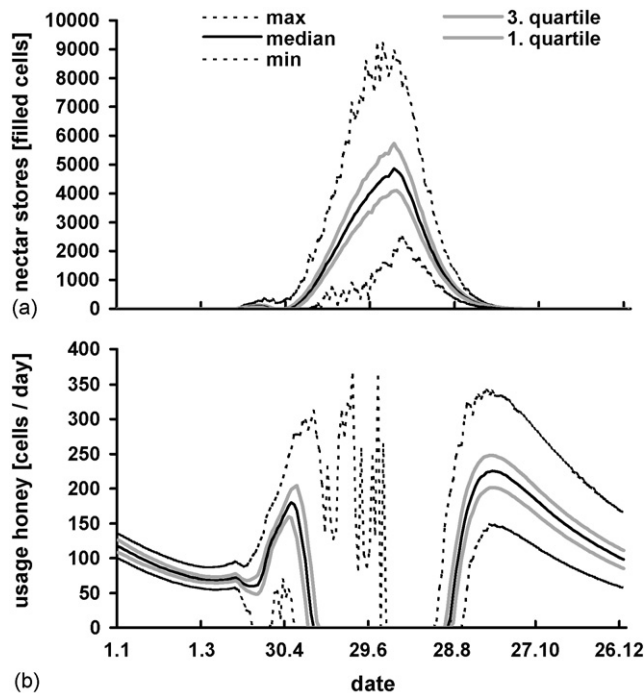


Fig. 6 – Seasonal dynamics of nectar stores (a) and honey usage (b) of a simulated honeybee colony throughout a year (median, maximum, minimum and quartiles of 1000 simulation runs; all parameters varied within a range of $\pm 15\%$).

- K4: the maximum level of honey stores (the honey stores peak);
- K5: the number of adult bees in winter (on day $t = 360$);
- K6: the level of honey stores in winter (on day $t = 360$).

We chose these criteria because we think that they are the most important to describe the survival rates and reproduction rates of honey bees on the colony-level.

Fig. 7 shows the results of the sensitivity analysis of four parameters that directly affect population size and structure. Fig. 7a shows the model's sensitivity to changes in the maximum egg laying rate (ELRbase): changes of $\pm 40\%$ in this parameter changed criteria K1, K2, K3 and K5 by up to $\pm 40\%$, criterion K4 by up to $\pm 22\%$, and criterion K6 by up to $\pm 18\%$. Fig. 7b shows the model's sensitivity to changes in all the mortality rates: when we simultaneously changed all mortality rates defined in the model by a multiplier (MULTIPLIERmortality(all-stages)) within the range $\pm 40\%$, the criterion that was most affected was K5 (+148 and -61%). K1 varied by +69 and -36% , K2 and K3 by +15 and -13% , and K4 and K6 by +72 and -39% . Fig. 7c shows the model's sensitivity to changes in the mortality rates of the brood. Again, we used a multiplier (MULTIPLIERmortality(brood)) within the range $\pm 40\%$ to affect mortality rates of all brood stages. All criteria (K1–K6) varied within the span of +21 and -16% . Fig. 7d shows the model's sensitivity to changes in the parameter FACTORothertasks: the two honey-based criteria K4 and K6 were most affected by changes in FACTORothertasks. They varied by +8 and -13% . The other criteria varied within +3 and -2% .

Fig. 8 illustrates the model's sensitivity to six parameters that directly affect the foraging tasks. Fig. 8a shows sensitivity to FACTORforagingmax, which represents the maximum fraction of adult bees that are associated with the foraging tasks. The honey-related criteria K4 and K6 are most affected by this parameter, and the effects were heavily asymmetrical. A parameter value 40% below the standard value changed K6 by -52% and K4 by -39% . A parameter value 40% above the standard value caused an increase of 14% in K6, and an increase of 10% in K4. K2 and K3 were almost unaffected ($\pm 0.1\%$). K1 and K5 were affected between +15 and -6% . Fig. 8b and c show the model's dependency on the parameters TURNSpollenforager and TURNSnectarforager. Both subfigures show the same pattern, only the scaling differs. In both cases, the honey-related criteria K4 and K6 are affected the most: variations in TURNSnectarforager in the range of $\pm 40\%$ caused variations in K4 and K6 up to +36 and -50% . Variations in TURNSpollenforager in the range of $\pm 40\%$ caused variations in K4 and K6 up to +7 and -18% . The other key criteria were affected by no more than +2.1 and -1.3% . Fig. 8d shows the model's sensitivity to the parameter FACTORpollenstorage: the pollen-related criterion K3 is affected strongly by changes in this parameter ($\pm 56\%$). The other criteria are affected within +9 and -16% . Fig. 8e shows the model's sensitivity to the parameter ProcessorsPerCell: again the two honey-related criteria were the most affected: K4 and K6 changed by +8 to -13% , while the other criteria changed by only +2.1 to -0.3% . Fig. 8f shows the model's sensitivity to the food consumption rates. We varied a scalar (MULTIPLIERconsumption) between 0.6 and 1.4 and used it as a multiplier for each consumption rate (pollen, nectar, brood, adults). Lowered consumption rates (-40%) increased criteria K6 (+45%) and K4 (+29%), while they decreased criterion K3 (-40%). Increased consumption rates (+40%) decreased K6 (-44%) and K4 (-28%), while they increased K3 (+40%). K1, K2 and K5 varied only within +0.5 and -0.6% .

4.4. Conservation of bees

In population modeling it is very important to ensure that there is "conservation of mass". In our model, we had to ensure that no bees are inadvertently "lost" during the simulation runs. So we collected all dead eggs, larvae, pupae and adult bees into the additional variables LOSTeggs(t), LOSTlarvae(t), LOSTpupae(t) and LOSTadult(t). Fig. 9 shows how the cumulative values of these control-variables develop over time in comparison to the cumulative input of bees into the model, that is ELR(t). In the simulation run, we started with 15,000 bees on model initialization ($t = 0$). At the end of the simulation run ($t = 365$), the cumulative input equaled almost exactly the sum of the cumulative losses of the final living bee population. The difference between those two final values, due to computer errors in calculating floating point numbers, was extremely small, 1.49×10^{-10} , less than one bee!

4.5. Population dynamics in small observation hives

In the prior sections, we massively compared our population model to empiric data in literature. These data were collected with human-made bee hives which provided enough

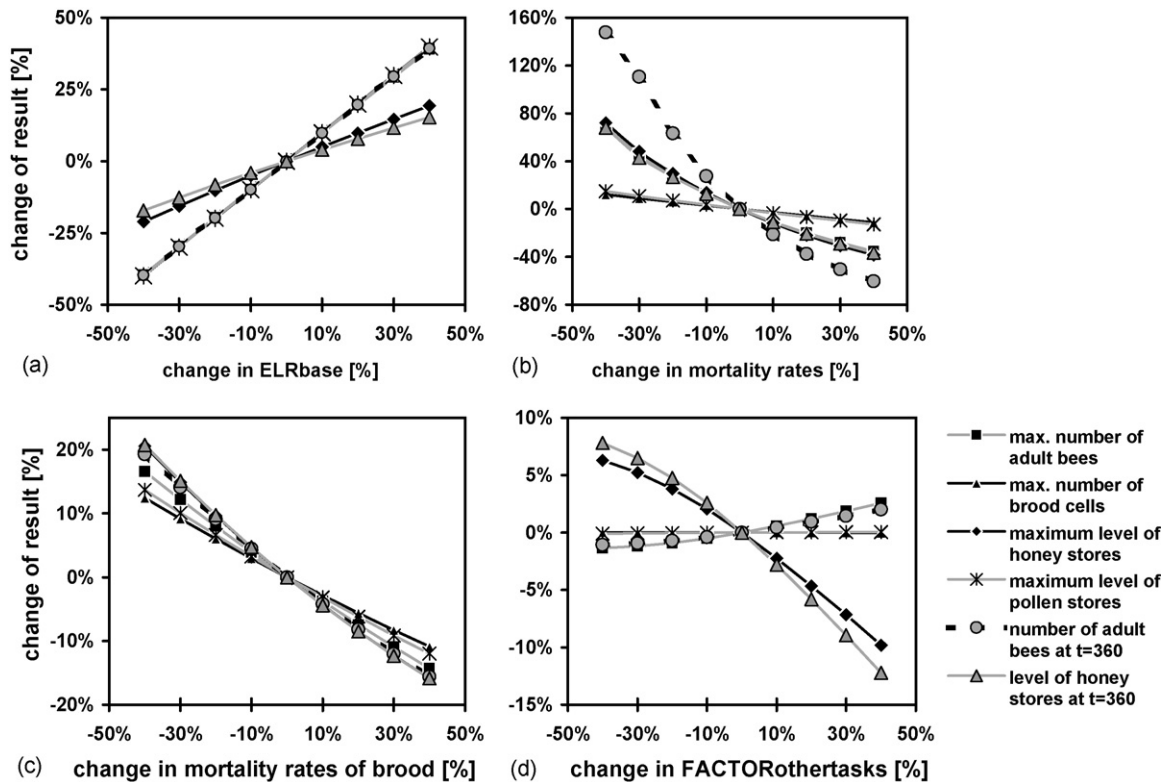


Fig. 7 – (a–d) Sensitivity analysis of the model—part 1. We varied the following parameters that directly affect the colony's age structure and task schedule within $\pm 40\%$ around the standard value: ELRbase, MORTALITYmultiplier(all stages), MORTALITYmultiplier(brood) and FACTORothertasks. On the Y-axis, the subgraphs show relative changes (in %) of the simulation runs. We used six criteria to measure the model's sensitivity to the varied parameters: maximum levels of adult bees, of brood, of pollen stores, and of honey stores, as well as the number of adult bees and the amount of honey stores at day t = 360.

space and (in most cases) also partially prebuilt comb material. Another type of bee keeping is performed by scientists, who keep colonies in small observation-hives (usually one to six frames). To demonstrate the influence of the available comb space onto the population dynamics, we performed a series of simulation runs with different constant values of $CELLShive \in \{20,000, 40,000, 65,000, 130,000\}$, the parameter that represents the number of available comb cells in the modeled colony. Despite the parameters $CELLShive$, the other parameters were set identical to the default settings, which were used for example for simulation runs depicted in Fig. 3 (median run). Fig. 10 shows the results of these simulation runs by depicting the daily amount of unsealed larvae during the breeding season. In small hives ($CELLShive = 20,000$), oscillations in the size of the open brood nest appear and the production of new brood stops due to the decreased empty space available for breeding. This also happens in long-term experiments in three-frame observation hives (approximately 20,000 cells of comb) with real bees, usually the experimenter removes sealed brood to allow new brood production in the hive. In hives bigger than those mentioned above those oscillations cannot be found at a significant level. Also the simulation does not predict such oscillations in bigger hives ($CELLShive > 40,000$). The timing and the extent of such space-induced oscillations depends mainly on the egg laying activity

of the queen (ELRbase, was set to 1400 in Fig. 10) and on the initial amount of honey in the colony ($STOREShoney[0]$, was set to 5000 in Fig. 10), because honey is a resource that consumes space in large amounts and for a long time in a honeybee colony. As can also be seen in Fig. 10, the produced total amount of brood per year decreases with decreasing hive size.

4.6. Population dynamics in wild-life bees

In nature, European honeybees usually live in cavities like hollow trees. These cavities usually provide less space than artificial bee hives can do. In addition to that, the bees have to produce the needed combs completely by themselves. In the annual life cycle, a honeybee colony reproduces in spring by producing one or several queens during a period of approximately 30 days before the swarming event. It is still not finally solved which factors determine whether a swarming is performed by a colony or not, but several factors were identified to increase the likelihood of swarming significantly: congestion of bees, accumulation of large amounts of food, high levels of sealed brood. During the weeks before swarming, the old queen increases her egg laying for some time. A few days before leaving the colony, the old queen ceases her egg laying and loses weight, what supports the flying with the swarm.

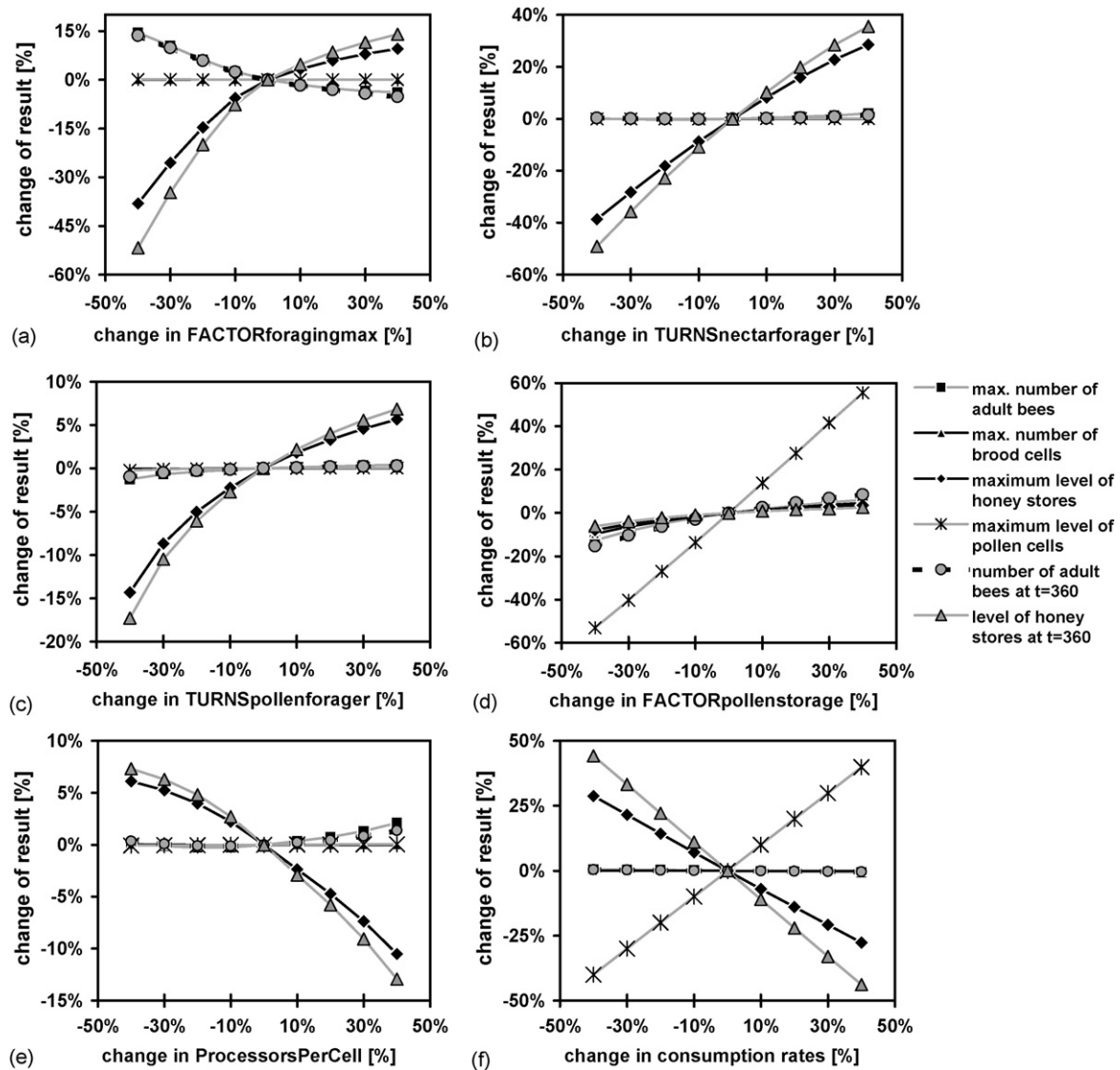


Fig. 8 – (a–f) Sensitivity analysis of the model—part 2. We varied the following parameters that directly affect the food management (foraging, storage and consumption of nutrients) within $\pm 40\%$ around the standard value: **FACTORforagingmax**, **TURNsnectarforager**, **TURNspollenforager**, **FACTORpollenstorage**, **ProcessorsPerCell** and **MULTIPLIERconsumptionrates**. On the Y-axis, the subgraphs show relative changes (in %) of the simulation runs. We used six criteria to measure the model's sensitivity to the varied parameters: maximum levels of adult bees, of brood, of pollen stores, and of honey stores, as well as the number of adult bees and the amount of honey stores at day $t = 360$.

At the swarming day, the queen leaves the old hive with approximately the half of the bees and the swarm searches a new site (cavity) for building up the new colony. The adult bees that follow the queen carry a full nectar load with them to provide the swarm with a small energy reserve. According to [Seeley \(1995\)](#), the swarm bees build approximately 20,000 cells of comb during the first days and the comb space increases to 100,000 cells, during the rest of the season. In the old colony, a new queen emerges in the meanwhile and has to perform several mating flight during the first days. Then the new queen can start to lay eggs. Both colonies, the old one and the newly founded one have to compensate a pause in brood production. The “hole” in the age demography is bigger in the newly founded colony, because in the old colony the old queen has

prepared a valuable stock of brood that emerges after the old queen has left the colony.

In the following section, we describe how small adaptations of the base model equations allowed us to use HoPoMo to model the population dynamics of both colonies involved in such a swarming process: the old remaining colony and of the newly founded one. In one simulation run, our model can only treat one colony. Because of this fact, we had to run the model twice during this analysis and we had to copy the number of swarming bees predicted by the first run (mother colony) as an input parameter into the second run (daughter colony). To provide an environment as nature-near as possible, we used real weather data of Graz (Austria) in 1998 instead of the “optimistic” weather functions used in $\text{Rain}(t)$ and $\text{TEMP}(t)$

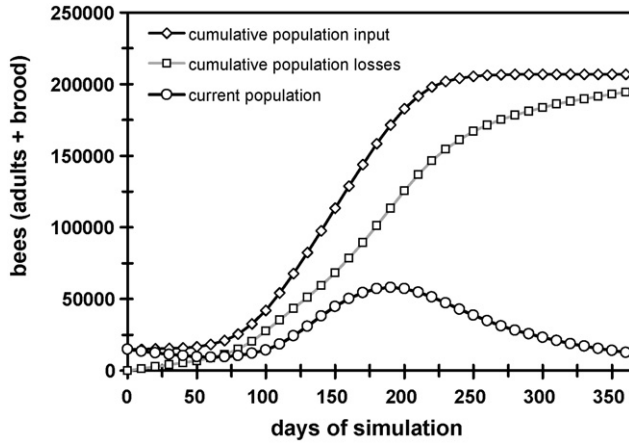


Fig. 9 – Analyzing the conservation of bees in the model. The figure plots the cumulative input of bees (egg laying rate $ELR(t)$, see Eq. (5)) and the cumulative losses of bees during the different developmental stages (see Eqs. (6), (11), (14) and (19)). At the end of the simulation, the cumulative input equals almost exactly the cumulative losses plus the final population in the hive. We noticed an extremely small computer calculation error (due to using floating point numbers) of 1.49×10^{-10} bees. This result demonstrates the validity of the model's structure.

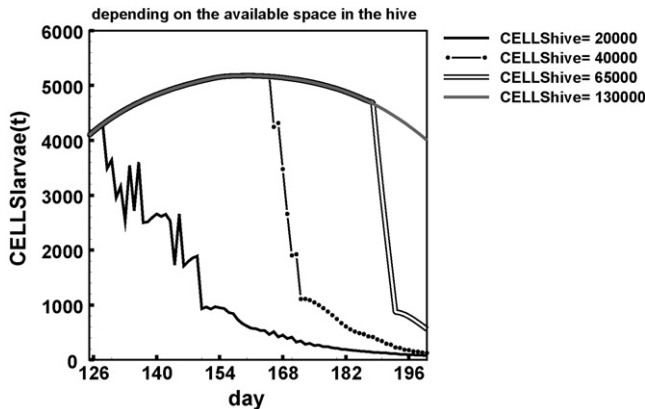


Fig. 10 – Simulation runs with different values of CELLShive. The run $CELLShive = 20,000$ corresponds to the situation in usual three-frame observation hives that are used for scientific experiments. The run with $CELLShive \geq 65,000$ corresponds to bigger bee hives, which are usually used for commercial bee keeping. The figure shows the emergence of oscillations of the unsealed brood nest size due to limited space for egg laying by the queen in runs with smaller hive sizes. Such effects are seen in long-term experiments with real bees (unpublished data). The time of emergence of these oscillations depends mainly on the mean egg laying rate of the queen ($ELRbase = 14,000$ eggs per day) and on the amount of nectar the colony had at the beginning of the year ($STOREShoney[0] = 5000$ cells). The figure shows data from day 126 to 196.

in the simulations described in the sections above, where we evaluated the “base model”.

4.6.1. Swarming extension, part 1: modeling the ‘mother colony’

The parameter swd (=“swarming day”) determines the day of the swarming event. In our simulation runs, we set $swd = 140$, what corresponds to the date of 19th of May. To produce a scenario of high congestion and a high amount of sealed brood for the swarming colony, we set $CELLShive = 125,000$ cells and $ELRbase(t) = 2000$ in this run for all $t < swd$. Please note that the former constant parameter $ELRbase$ was converted into a time dependent parameter $ELRbase(t)$. The new queen has usually a lower egg laying activity in the first season ($ELRbase(t) = 1200$ for all $t \geq swd$) and the old queen produces more eggs in the weeks before swarming. To model these facts, we introduce a new $FACTORqueen(t)$, which is multiplied to the right hand side of Eq. (5):

$$FACTORqueen(t) = \begin{cases} 1.2, & \text{if } (swd - 30) \leq t < (swd - 3) \\ 0, & \text{if } (swd - 3) \leq t < (swd + 14) \\ 1, & \text{else} \end{cases} \quad (61)$$

$$ELRbase(t) = \begin{cases} 2000, & \text{if } t < swd \\ 1200, & \text{else} \end{cases} \quad (62)$$

$$ELR(t) = ELRbase(t) \cdot (1 + ELRstoch(t)) \cdot (1 - season(t))$$

$$\cdot SUPcomb(t) \cdot FACTORqueen(t) \quad (5a)$$

The number of bees that leave the swarm on day $t = swd$ can be calculated ($BEESSwarm(t)$) by the new Eq. (63), what of course also affects the number of adult bees that remain in the colony (calculated by Eq. (19)). We assumed that 60% of the available adult bees leave the hive with the new swarm, what represents a usual absolute swarm size (according to Fell et al., 1977, see details below).

$$BEESSwarm(t) = \begin{cases} BEESSadult(t - 1) \cdot 0.6, & \text{if } t = swd \\ 0, & \text{else} \end{cases} \quad (63)$$

$$BEESSadult(t) = (BEESSadult(t - 1)$$

$$+ PUPAE(LIFESPANpupa, t - 1))$$

$$\cdot (1 - MORTALITYadult(t)) - BEESSwarm(t)$$

$$(19a)$$

The bees that leave the hive take a certain amount of food (honey) with them, what has to be considered in the calculation of the daily honey stores. We also want to consider the fact that honeybees forage more intensive for nectar in times when they have a high number of empty comb cells available in their colony. Therefore, we replaced the former constant parameter $TURNsnectarforager$ by a variable $TURNsnectarforager(t)$, which considers the ratio of empty cells to

filled cells within the colony (see Eq. (64)). The honey carried away by the swarm bees is calculated by Eq. (65), the value of $LOSS_{honey_swarm}(t)$ has to be considered as an additional consumption of the honey by a small modification of Eq. (56).

$$TURNS_{nectarforager}(t) = 15 + 7 \cdot \left(\frac{CELLS_{empty}(t-1)}{CELLS_{hive} + 1} \right) \quad (64)$$

$$LOSS_{honey_swarm}(t) = \begin{cases} \min \left\{ \begin{array}{l} STORES_{honey}(t-1) \\ BEES_{swarm}(t) \cdot LOAD_{nectarforager} \end{array} \right\}, & \text{if } t = swd \\ 0, & \text{else} \end{cases} \quad (65)$$

$$USAGE_{honey}(t) = \min \left\{ \begin{array}{l} STORES_{honey}(t-1) \\ ((NEED_{nectar}(t) - USAGE_{nectar}(t)) \cdot RATIO_{nectar_to_honey}) + LOSS_{honey_swarm}(t) \end{array} \right\} \quad (56a)$$

To check the plausibility of the results of our model extension, we compared the results to literature data: the dynamics of the adult bee population and of colony weight is depicted in Fig. 11c and d. Our simulations predicted a swarm of 10,310 bees leaving the hive on day $t=140$; the simulated swarm took a load of 412.4 cell-fuls of honey with it. This is in good agreement with the data given in Fell et al. (1977), who report the size of swarms they measured within 1 year to be between 2400

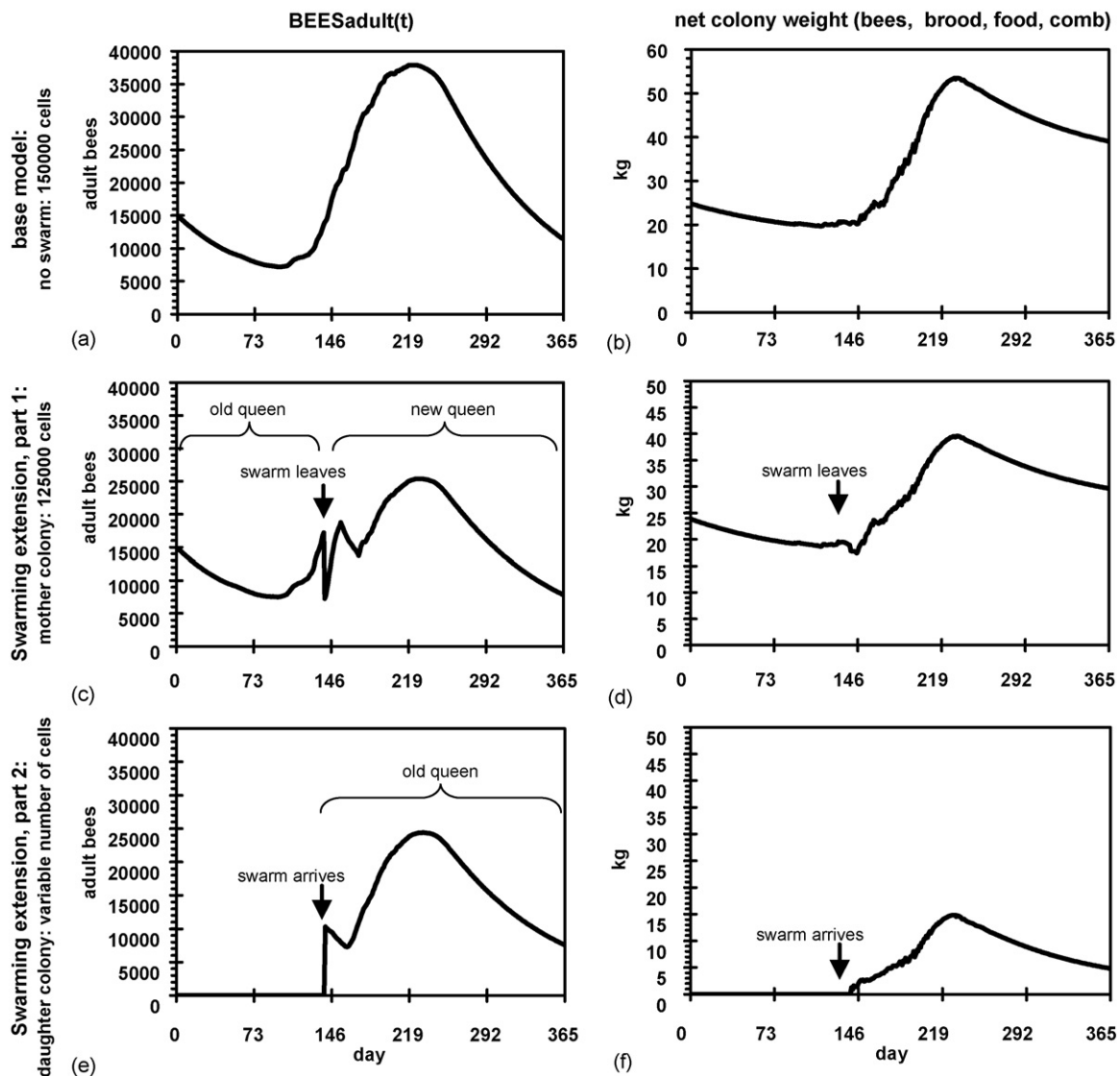


Fig. 11 – Results of the swarming extension: three simulation runs of our model. (a and b) A colony that has little congestion (moderate egg laying rate, much comb space) and does not swarm. (c and d) A colony that has high congestion (high egg laying rate, little comb space) and does swarm on day $t=140$. (e and f) The newly founded colony resulting from the swarm that left the colony depicted in (c) and (d). All runs were performed by using real weather data (rain and temperature) measured in Graz, Austria in 1998.

bees and 41,000 bees and an average swarm size of 11,800 bees. In Fig. 11c two minimum-“peaks” are seen as result of the swarming event, one is the effect of the sudden loss of adult bees when the swarm leaves the hive, the other one is at the moment in time when the pause in egg production shows its maximum effect.

4.6.2. Swarming extension, part 2: modeling the ‘daughter colony’

For modeling the daughter colony, we set all variables that describe masses (bees, brood, honey, nectar, pollen, hive cells) to 0 for all days $t < \text{swd}$. On day $t = \text{swd}$, the swarming bees arrive to the new site (we assumed no losses of bees and encounter of a new nesting site within the same day) and $\text{SWARMbees}(t)$ and $\text{LOSShoney_swarm}(t)$ are added to $\text{BEEsadult}(t)$ and to $\text{STOREShoney}(t)$. Furthermore we assumed that the old colony takes some time to reach full egg laying rate (see Eq. (61a)) and that $\text{ELRbase}(t)$ of the old queen is on a low maximum level of 1200 eggs per day. According to Seeley (1995), the bees build up 20,000 cells within a period of “a few days” and then manage to extend the comb to 100,000 cells during the rest of the season. According to (Hepburn, 1986, cf. Seeley, 1995), the production of 1 g of wax needs up to 6 g of sugar. Based on our own weightings of empty wax combs, we calculated a factor of $\text{RATIONectar_to_wax} = 0.66$ cellfuls. The growing comb was modeled as described in Eq. (67), the honey expenditure was implemented as an addition to $\text{NEEDnectar_adult}(t)$ (see Eq. (42)). Please note that the former constant parameter CELLShive is now converted into a time dependent variable $\text{CELLShive}(t)$ and that this replacement has to be applied to several equations in our model (Eqs. (2), (3), (59) and (64)). In our model, the workforce of comb builders is considered to be included into the constant factor FACTORothertasks . Fig. 11e and f shows the dynamics of the adult population and of the colony weight of the newly founded daughter colony.

$$\begin{aligned} &\text{FACTORqueen}(t) \\ &= \begin{cases} 0, & \text{if } t \leq \text{swd} \\ \text{FACTORqueen}(t-1) + 0.2, & \text{if } \text{swd} < t \leq (\text{swd} + 5) \\ 1, & \text{if } t > (\text{swd} + 5) \end{cases} \end{aligned} \quad (61a)$$

$$\begin{aligned} &\text{NEEDnectarbuilding}(t) \\ &= (\text{CELLShive}(t) - \text{CELLShive}(t-1)) \cdot \text{RATIONectar_to_wax} \end{aligned} \quad (66)$$

$$\begin{aligned} &\text{NEEDnectar_adult}(t) \\ &= \text{BEEsadult}(t) \cdot \text{NECTARNEEDadult} \\ &+ \text{NURSES}(t) \cdot \text{NECTARNEEDnurse} \\ &+ \text{FORAGERSactive}(t) \cdot \text{NECTARNEEDactiveforager} \\ &+ \text{NEEDnectarbuilding}(t) \end{aligned} \quad (42a)$$

$$\begin{aligned} &\text{CELLShive}(t) \\ &= \begin{cases} 0, & \text{if } t \leq \text{swd} \\ \text{CELLShive}(t-1) + \frac{2000}{7}, & \text{if } \text{swd} < t \leq (\text{swd} + 7) \\ \text{CELLShive}(t-1) + \frac{8000}{90}, & \text{if } (\text{swd} + 7) < t \leq (\text{swd} + 97) \\ \text{CELLShive}(t-1), & \text{if } t > (\text{swd} + 97) \end{cases} \end{aligned} \quad (67)$$

5. Discussion

5.1. Simulation results and model analysis

The model presented here is able to project the dynamics of a honey bee colony very realistically. The dynamics of the adult bee population (Fig. 3a) and the brood population (Fig. 3b) are very similar to those reported in the literature (Bodenheimer, 1937; Omholt, 1986; Fukuda, 1983; Bretschko, 1995; Bühlmann, 1985; Kunert and Crailsheim, 1988). Also the predicted dynamics of pollen stores and honey stores mimic literature data (Jeffrey and Allen, 1956). Unfortunately, we found no published data on honey stores (measured in cells) to compare with our simulated honey dynamics (Fig. 4b). To allow comparison with literature data, we calculated the weight of our simulated colony for each day by considering a base weight for the hive and the comb (15 kg) and adding the weights of the adult bee population, the brood and the nutrient stores (Eq. (59)). The projected seasonal pattern of our colony’s weight fitted well to literature data (Seeley, 1985), although feeding real data about environmental nectar availability would certainly improve the model’s performance in predicting the nectar income and the final level of the honey stores (see Fig. 4c).

The model was shown to be especially sensitive to mortality rates (Fig. 6b), which is quite usual for a population model. This finding is consistent with the model analysis presented by Omholt (1986). When we kept the mortality rates and the egg production rate fixed and varied only the other parameters ($\pm 15\%$), we found very low sensitivity of the model (Fig. 5). The factors FACTORforagingmax , $\text{TURNSpollenforager}$ and $\text{TURN-Snectarforager}$, which are all related to the foraging task, affect the model’s predictions only if the values are significantly lowered (Fig. 7a–c). Even then, only the level of honey stores is affected strongly. This shows that the model is able to simulate the regulation of pollen foraging according to a homeostatic set point in a plausible way (Schmickl and Crailsheim, 2004a). None of these foraging-related parameters affects the population dynamics (adults and brood) to a biologically significant extent. Overall, the food consumption rates of bees as well as the mortality rates used in our parameterization are very similar to empirical data given in literature (Alfonsus, 1933; Fukuda and Sakagami, 1968; Sakagami and Fukuda, 1968; Harbo, 1993).

The influence of limited hive space, a usual situation in observation hives used in scientific experiments, onto population dynamics was shown in an exemplary simulation run (see Fig. 10). The emergence of oscillation is predicted due to the fact that mostly honey (or nectar) and brood compete for empty space. Only after a significant fraction of brood

emerges from the pupal stage or after a significant amount of honey got consumed, new space for new egg laying is available. Such a scenario, especially the “competition” for empty space between brood and nectar/honey is described by Camazine et al. (1990) in a spatial model (based on individual cells on a comb) of a honeybee brood comb. Our results, derived from a non-spatial model fit perfectly to the proximate mechanisms suggested in the article of Camazine et al. (1990).

By slightly modifying some model equations and by adding few variables, we were able to simulate wild-living swarming honeybee colonies. The population dynamics of both, of the old colony (with the new queen) and of the new colony (with the old queen) was modeled in a combined simulation run. This demonstrated the wide applicability of our model and gives perspectives to use the model for investigating scenarios with many colonies reproducing in a shared environment. So far the user of the model has to decide whether or not a swarm leaves a modeled colony, but these decisions are thought to be implemented in later versions of the model as result of feedbacks that are provided by the congestion of bees and by the resource status of the colony.

5.2. The modeling approach and technical issues

The model was built from a step-by-step derivation of difference equations based on much biological data. The way the model was constructed allows us to address many biological and practical questions: it allows us to predict the effects of colony treatments (addition or removal of pollen, honey, adult bees or brood) on colony development. By modifying Eq. (16), for example, we can investigate the effects of pollen traps. By modulating the mortality factors (e.g., in Eq. (10) or Eq. (18)), we can analyze how colony development is affected by bee diseases. Also, the effects of different environmental situations can be studied by modifying Eqs. (20)–(25). An important feature of the model is that it incorporates published data at the level of individual bees, e.g., the parameters FACTOR_{foragingmax}, TURN_{Spollenforager}, TURN_{Snectarforager}. The model incorporates several very important feedback loops that are present within the honeybee colony, so we can investigate the effects of proximate individual behavior on global colony-wide results (e.g., population development, development of nutrient stores). This article analyzes the global properties of the model and tests its validity against literature data. Several applications of the model are demonstrated within this article (commercially controlled colonies, bees in observation hives and wild-living bees), additional applications of the model involving the topics mentioned above will be published in separate articles.

With 60 equations for the basic version, the model is rather complex. To give the reader an easy overview of the model, Fig. 12 shows a “stock-and-flow” diagram of the most important feedback variables that we used in the model. The figure shows the flow of material through the model and indicates the most important causal relationships among the most important model variables: these are those dependencies that form the major feedback loops. In the upper left corner of Fig. 12, the feedback loops that regulate the available empty cell space in the colony are shown: high levels of brood population and/or high levels of nectar and honey stores lower

the egg laying rate of the queen and restrict the nectar foraging. In the lower left corner, the main factors of pollen consumption are shown. A lack of pollen stores or a lack of nursing bees increases brood cannibalism and regulates the brood levels according to the current demographic situation and according to the current pollen status (lower part, middle). The negative feedback of pollen stores onto pollen foraging regulates the pollen stores in a homeostatic way around a set point. On the lower right part of the figure, the task selection process is shown in a very reduced manner. On the one hand, higher levels of adult population increase the number of bees associated to the modeled tasks. On the other hand, these task assignments increase adult mortality and the consumption of nectar, honey and pollen, depending on the kind of task. If this additional resource consumption is not compensated by a higher income of resources, the number of adult bees is reduced via brood cannibalism in a delayed manner. As can be seen in the upper right part of the figure, there is no negative feedback regulating the collecting of nectar, except via the regulation via cell space, which acts only in case of a colony that has nearly totally filled comb cells. In most situations, almost all workforce that is available in excess is designated for nectar collection. Thus, the two most important factors that regulate the nectar collection of the colony are the size of the adult population and external factors (season, weather). The processing of nectar into honey binds a certain amount of the available workforce, but the loss of stored volumes relaxes the negative feedback loop that inhibits nectar collection according to the filling status of the combs.

The analysis of the cumulative input of bees (egg laying rate) and of the cumulative losses of bees (mortalities) shows a final error of 1.49×10^{-10} bees. This can be explained by the numerical errors that arise when computers calculate floating point numbers. For practical usage of the model, this error can be neglected.

Many population models use differential equations to describe how variables change over time. We used difference equations with $\Delta t = 1$ day because our model describes only the seasonal pattern in the modeled variables. We did not require finer time intervals than 24 h. We recognize that there is also an underlying diurnal pattern in the dynamics of these variables in nature: as pollen and nectar influx is zero throughout the night, nectar, honey and pollen stores decrease throughout the night periods. During daytime in good weather, foraging activities and resource influx show positive values, and resource stores usually increase. Rather than focusing on the diurnal patterns in the population dynamics and resource dynamics of a honeybee colony, we sought to create a model that describes the seasonal patterns and the effect of colony treatments within time windows of several days or weeks. The population data and the resource status of our real honeybee colonies are also assessed in time intervals of 1 day. In contrast to the model presented here, Schmickl and Crailsheim (2004b) present a separate model that shows and explains the dynamics of honey stores throughout a foraging day.

The time resolution into 1-day-wide steps proved to be sufficient to model the dynamics of a honeybee colony. Only when we set the value of TURN_{Snectarforager} or of LOAD-

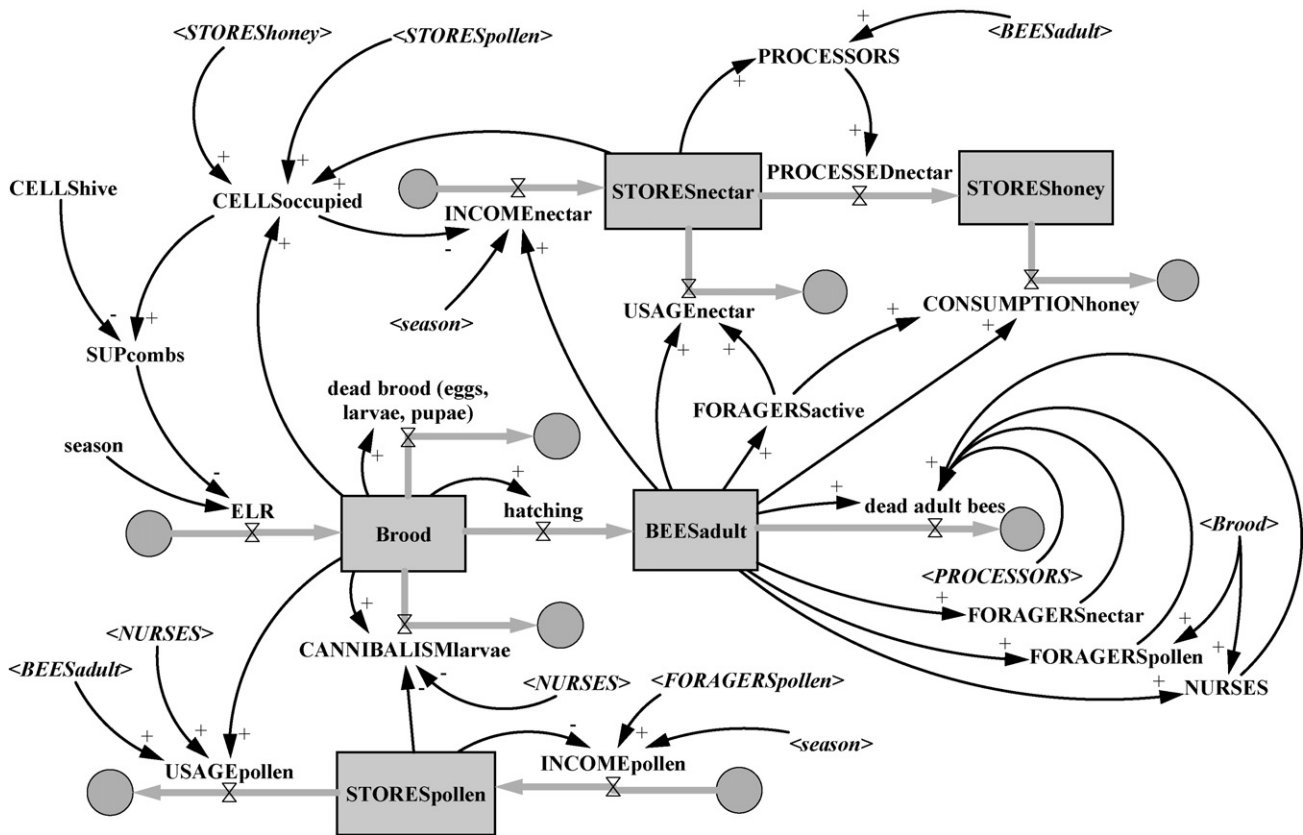


Fig. 12 – A stock-and-flow diagram of the most important components of our model. The diagram depicts the flow of materials (brood, adults, nectar, honey, and pollen) through our model: grey boxes indicate model variables that indicate one kind of material. Grey thick arrows indicate possible flows of material. Grey circles indicate sources and sinks, through which material enters or leaves the model. Black arrows indicate “causal relationships”, a plus sign or a minus sign indicates whether an increase in one variable causes an increase or a decrease of another variable. Please note that we showed only the most important feedback loops in this diagram and that in the model the influence of one variable onto another variable often acts through several “intermediate” variables that are not shown in this diagram. For the sake of simplicity, we combined all immature stages (EGGS, LARVAE and PUPAE) into one stock called “brood”.

nectarforager to high values, did we observe the emergence of oscillations in the recruitment of nectar foragers and of nectar processors. These oscillations were not numeric artifacts; the system simply turned to an alternation of nectar foraging and nectar processing. In nature, the balance between nectar processing and nectar foraging is established by a system of queuing delays at the scale of seconds (Anderson and Ratnieks, 1999; Ratnieks and Anderson, 1999; Anderson, 1998; Seeley, 1992, 1989; Seeley and Tovey, 1994).

5.3. Restrictions of the model

As already stated above, the time-step size of $\Delta t = 1$ day restricts our model to investigations of processes that work within periods that last at least for 1 day. Practically, we would favor the model for investigating periods that last between 1 week and 1 year. So far, we do not suggest to use the model to simulate a period of more than 1 year, because in nature, the egg laying of the queen changes from year to year, as the queen gets older, a fact that is not implemented in our model so far. Our model incorporates no spatial resolution of the comb

space, thus questions that address the spatial organization of the colony should be addressed with different approaches. Finally, we did not treat individual bees, we modeled cohorts sizes of workers that are performing a special task on each day. Our model describes how workforce flows between these cohorts from day to day, thus it is a clear top-down approach that we chose. For questions that address the plasticity of individual bees, we suggest to use an individual-based model that was build in the bottom-up approach. Finally, we want to state here, that the model can hold for honeybee colonies living under very extreme conditions, but only with extremely specific parametrization. Such extreme situations are: e.g., colonies in heat stress, colonies in extreme nectar dearth, colonies with an ill or old queen. These restrictions are also due to the fact that the management of water as a resource is not part of the model, that thermoregulation is not implemented and that processes like queen-superscedure are not modeled yet. The following section gives an overview about other models that have been published so far and how these models differ in their approaches from the model presented here.

5.4. Comparison to other published models

Several mathematical models are already published on the topic of honey bees. The majority of these articles focus on behavioral aspects of foraging (Schmid-Hempel et al., 1985; Seeley et al., 1991; de Vries and Biesmeijer, 1998; Gheorghe et al., 2001; Cox and Myerscough, 2003; Sumpter and Pratt, 2003; Bertram et al., 2003; Schmickl and Crailsheim, 2004b; Thenius et al., 2005), on food processing and associated queues (Anderson and Ratnieks, 1999; Ratnieks and Anderson, 1999; Anderson, 1998; Seeley and Tovey, 1994; Gregson et al., 2003), or on thermoregulation (Watmough and Camazine, 1995; Sumpter and Broomhead, 2000). Other models also focus on the processes involved in division of labor (in detail reviewed in Beshers and Fewell, 2001) or on spatial organization in honeybee colonies (Camazine et al., 1990). Population models of social insects have been published by Omholt (1986, 1992) and by Harris (1995). Dolejsky and Schley (1980) and Martin (1998) combined a honeybee population model with a population model of a bee parasite (*varroa* mites). This honeybee parasite was also treated in a population model by Sumpter and Broomhead (2001). Martin (1991) developed a model for wasps, which is similar to the model presented here in some aspects (e.g., the time resolution).

DeGrandi-Hoffman et al. (1989) presented a model called BeePop, which models the egg laying of the queen depending on adult population size, as it was already demonstrated in the article of Omholt (1986), by the daily temperature and by the photo-period. The model concentrates on the queen's egg laying and the derived population structure. As within the older and less complex models of Bodenheimer (1937) and Fukuda (1971), the models of Omholt and the model of DeGrandi-Hoffman model the task allocation between house bees (nurses, processors, builders, ...) and field bees (foragers) purely based on the age of the bees, without considering outside factors (weather, botanical factors) and inside feedbacks (demands). Another very complex model, named AHBsim, was published by Makela et al. (1993). This model extended the concept of the honeybee population model to a new level: they modeled the spread of colonies within a given environment via swarming and the spread of colony-level properties via modeling an abstract "genome" of the queens and drones. In this case, the egg laying activity of the queen depends on the number of workers, on day-length and on the daily temperature. In contrast to all other published models, a variety of honeybee working tasks is modeled and jobs are assigned in a priority based system. The way these priorities are assigned to tasks differs significantly between HoPoMo and AHBsim: in HoPoMo, two high-priority tasks are modeled, which are brood nursing and pollen foraging. The task of nectar processing has a medium priority and the task of nectar foraging has the lowest priority. Pollen foraging has low priority in AHBsim, what is contradictory to findings of Lindauer (1952), who demonstrated that pollen deprivation can assign up to 82% of all foragers to the task of pollen foraging. Additionally nectar storage is of the same low priority as nectar foraging, what is contradictory to the findings of Seeley (1989, 1992), who showed how longer waiting times of foragers lead to the additional recruitment of nectar receivers and inhibit the further increase of the cohort of active foragers. Nevertheless, AHBsim

was the first honeybee model that used a sort of individual-based modeling for a honeybee population model, although it was no pure multi-agent model. Interestingly, the addition of individual genomes leads to an outstanding combination of individual-based modeling to a sort of "genetic algorithm" or "evolutionary strategy".

What makes our model different from other models is the fact that we combined very detailed aspects of population development, including cannibalism of brood (when there is low food influx or an inadequate nursing workforce) and task-related mortality rates, with a detailed model of resource management and division of labor. Our model is analyzed by exhaustive sensitivity analysis, sensitive parameters were discriminated from the less sensitive ones (see Figs. 3–8) and simulation results were compared to empiric data. We show simulation runs throughout a full year.

Honeybees play an important ecological role as pollinators, and pollination units are widely commercially used in agriculture. The efficiency of these units is often increased by the usage of pollen traps, which stimulate the bees to more pollen foraging, what leads to more (or better) pollination. The model described here is the very first in literature that deals with the important feedback loop that links pollen supply to brood survival (cannibalism), brood production to age demography, and age demography to the division of labor. These important aspects are neglected by all mathematical population models on honeybees so far, but they are reviewed in detail by Schmickl and Crailsheim (2004a). Cushing et al. (1998) used an age-structured model to demonstrate the importance of cannibalism in the population dynamics of another insect species. However, contrary to their example of *Tribolium confusum*, where cannibalism leads to chaotic oscillations, the cannibalism in eu-social insects enforces the colony's stability. By cannibalizing brood that cannot be nursed sufficiently, the colony achieves a homeostatic regulation of the supply-to-demand ratio (Schmickl and Crailsheim, 2001). Our model gives a detailed description of demography throughout a full year (including winter). Our model not only tracks the number of bees, it also tracks their "function" through a "behavioral" component that models a honeybee colony's ability to adapt nursing efforts, nursing efficiencies and foraging efforts according to the current demand. The model also implements a resource management factor concerning the pollen stores, based on the descriptions in literature. The daily resource and demand state in the model also provides feedback on the colony's population development. Our model is one of the most detailed population models that has yet been published for social insects, especially the topics of brood cannibalism due to pollen hunger or due to a bad nurse-to-brood ratio are implemented in a very detailed manner.

5.5. General final comments

HoPoMo is a very general model of honeybee population dynamics. The way the model is formulated, it is easy to account for several colony manipulations that are common in scientific experiments or in commercial bee keeping. By extending (in most cases) just one of the model equations, we can (and will) treat any of the following: pollen traps, queen caging, brood removal, pollen removal and honey removal.

This way, the model can serve as a valuable tool in developing experimental setups, because it is able to predict the expected colony status after a combination of treatments. We will extend the model into several directions to allow modeling of the effects of parasites and of bee diseases. These extensions will build onto HoPoMo, as it is described and analyzed in this article, the extensions will be published with the same level of details as HoPoMo is described here. We demonstrated that the base model is able to depict the population development of very small honeybee colonies that are used in scientific experiments without any adaptations of the model equations. In addition to that, we demonstrated how easy it is to build on the presented model by extending the model to allow the modeling of swarming wild-life honeybees. We had to add 7 very simple equations to treat swarm-specific system variables and we had to add 5 trivial additions to existing model equations. We suggest HoPoMo as a basic framework for honeybee population modeling and why we wanted to give all necessary information the reader needs to build on this foundation (all equations, all parameters, all constraints and comparisons to empiric data).

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