



Eidgenössische Technische Hochschule Zürich  
Swiss Federal Institute of Technology Zurich

# Lecture with Computer Exercises: Modelling and Simulating Social Systems with MATLAB

Project Report

**Hive Simulation**

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## Abstract

In this article, we present a model that simulates the behaviour of a single colony of honey bees (*Apis mellifera*) living in a beehive and interacting with its environment. Three different kinds of bees were implemented: The forager, the scout bee and the hive bee. The hive is a quantitative model largely based on the works of *David S. Khoury et al.* [1], using a range of differential equations to represent hive growth, social inhibition, food availability and bee ageing. The focus of this model lies, in contrast to *Khoury et al.*, in the hive's interaction with the environment. Our objective is to find more about the hive's relation to the seasonal changes (no food income in winter, different flowers each month). To simulate seasons, a fine-grained and easily extensible environment algorithm is used, in which the bees navigate and collect food. For the development of the environment simulation, empirical observations by *T.D. Seeley* [2] were used.

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## 1 Individual contributions

We discussed and extended the model together on a weekly basis, collecting and mixing individual ideas. The report was written in a cooperative manner. Every team member wrote the sections according to their *individual tasks* and then corrected and extended the sections of the other two members. The individual tasks have been assigned by taking into account the programming skills, personal interests and available time.

### Individual tasks:

- *Stefan Gugler, BSc Interdisciplinary Sciences:* Interpretation and application of empirical data in the basic and advanced model. Searching references and data in the literature.
- *Elias Huwyler, BSc Computer Science:* MATLAB scripts for map generation, map loading and data plotting. Interpretation and analysis of the simulation results.
- *Fabian Tschopp, BSc Computer Science:* Implementation of the basic and advanced model in MATLAB (object oriented structure, code hierarchy, actual implementation).

## 2 Introduction and Motivations

The global decrease of honey bee populations (*Apis mellifera*) is not only conspicuous, but also alarming. Our dependency on pollination in almost all forms of agricultural cultivation (such as fruit and vegetables, spices, nuts etc.) urges us to find out more about the bee's behaviour and their mortality. In recent years, many studies [3] [4] have been carried out to find out the reasons for the mass decline of pollinators: diseases, destruction of the environment, pesticides/fungicides (such as *imidacloprid*, *deltamethrin* [5], *fipronil* [6], and many others) and maybe even climate change [7]. The sum of all these factors culminates in the mass death of bees and can lead to a serious economic crash as well as to a impairment of agricultural resources. This motivated us to develop a simulation to find crucial situations in which the hive's health becomes unstable and does not survive, specifically regarding environmental influences (i.e. annual shift of seasons). We started with an existing simulation by *Khoury et al.* [1] and extended it with knowledge and empirical data from *T.D. Seeley* [2].

### 3 Description of the Model

#### 3.1 Basic model: Hive simulation

Our model is widely based on the studies and equations of *D.S. Khoury et al.* [1]. We used his quantitative models (equation 1 to 6) as described bellow and added new parameters to find out more about the bee's behaviour.

Food, seasons, brood, foragers and hive bees are the key elements of our model. The dynamics of the hive is based on the bee's behaviour and their interaction with the environment as well as natural influences, i.e. seasons (which are separately added to *D.S. Khoury's* model). Food here means nectar and pollen, which are - according to *D.S. Khoury* - not further distinguished to keep the model simple (see chapter 5.4.4). After the queen lays an egg, a larvae develops inside a honeycomb cell. The equations show the proportionality of the brood to the food income and the relations to the number of bees. Neglecting the complex process of reaching adulthood, we assume, according to *D.S. Khoury*, that larvae become adult hive bees 12 days after pupation. The mortality rate of hive bees or capped brood is negligible if there are no specific diseases implemented. The agents are only female bees, since they are responsible for maintenance and sustainability of the hive and the foraging process. The males are ordinary hive bees. With all this information we can firstly set up the equation for the brood number change:

$$\frac{dB}{dt} = LS(H, f) - \varphi B \quad (1)$$

It associates different factors to the brood number.  $L$  is the laying rate of the bee queen and  $S(H, f)$  is a function of the survival rate dependent on the amount of food  $f$  and the number of hive bees  $H$ .  $\varphi$  is the adult bee emerging factor and  $B$  represents the brood. The equation gives us the survival rate of the brood.  $S(H, f)$  is modelled as follows:

$$S(H, f) = \frac{f^2}{f^2 + b^2} \frac{H}{H + v} \quad (2)$$

The variable  $v$  indicates the effect of the hive bees on the brood, whereas  $b$  shows the food effect on brood survival. It decreases as food increases. As  $f$  and  $H$  become very large,  $S(H, f)$  becomes constant. The first factor is a sigmoid function and shows the correlation of the food available and the capped brood. A decrease in brood can occur because of lack of food (they cannot be fed) and / or because adult bees consume the larvae to keep the resources for the hive and recycle the proteins (cannibalism). The second factor models the interdependency of the hive bee numbers on the survival of the brood. If there are large stores of food but no hive bees that can provide the food to the larvae, the brood survival also declines.



The second differential equation describes the rate at which the number of hive bees changes:

$$\frac{dH}{dt} = \varphi B(t - \tau) - HR(H, F, f) \quad (3)$$

$\tau$  is the ageing time and  $\varphi B(t - \tau)$  is the rate at which adult bees develop from pupation to adult bees (emergence rate).  $H$  is again the hive bee number, the last term is the recruitment function and given as

$$R(H, F, f) = \alpha_{min} + \alpha_{max} \left( \frac{b^2}{b^2 + f^2} \right) - \sigma \left( \frac{F}{F + H} \right) \quad (4)$$

This function models the change from a hive bee to a forager bee.  $\alpha_{min}$  denotes the transition when there is enough food but not much foragers. Vice versa,  $\alpha_{max}$  is used for less food. As before,  $b$  is the food effect on brood survival and  $f$  is the amount of food.  $\sigma$  is the strength of social inhibition and is dependent on the number of foragers and hive bees.

The third differential equation correspondingly describes the rate at which the number of foragers changes:

$$\frac{dF}{dt} = HR(H, F, f) - mF \quad (5)$$

The mortality rate  $mF$  indicates the rate  $m$  at which the foragers  $F$  die. The recruitment function is the same as above.

The fourth and last equation tells us the rate of food change in the hive's stores. Foragers and hive bees are treated equally because their consumption is, according to *D.S. Khoury*, almost the same.

$$\frac{df}{dt} = cF - \gamma_A(F + H) - \gamma_B B \quad (6)$$

where  $c$  describes the average food a single forager collects per day.  $\gamma$  is the consumption of adult bees ( $A$ ) and brood ( $B$ ). In our extended model, we implemented an actual environment simulation so that the food income changes over time (see chapter 3.3). Equation 6 is then replaced by equation 11, which uses the daily food income instead of a fixed rate  $c$  per forager.

With those four differential equations, the change of brood (1), change of hive bee number (3), change of foragers (5) and change of food store (6) and the functions of the brood survival rate, correlating to the hive bee number and the food store (2) and a recruitment function (4), we can simulate a basic model of a hive with its interactions and changes. So far, it is identical with *D.S. Khoury's* model.

### 3.2 Changing laying rate over seasons

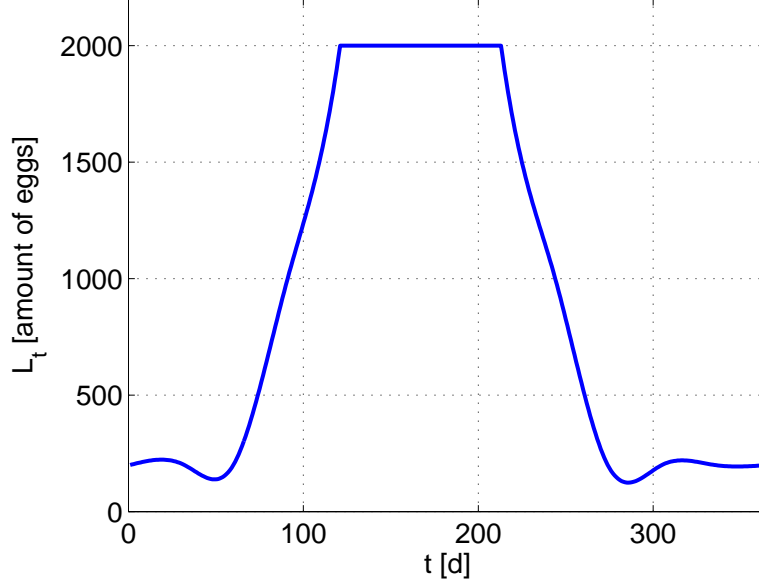


Figure 1: *The laying rate of the bee queen plotted over a year. The amount of eggs is capped after 2000 eggs.*

To make the model more realistic, equation 1 is replaced by equation 7. This incorporates that the bee queen does not have a constant laying rate. Instead, interpolated values based on *Wisdom of the Hive*, p. 34 [2] are used for the laying rate  $L_t$  (see fig. 1). *T.D. Seeley* denotes that the queen starts reproducing by early spring. We assumed that reproduction between April/May and October is realistic, as we obtained similar numbers of bees in summer (maxima) and winter (minima) to the empirical data of *T.D. Seeley* [2]. The minimal laying rate of 200 eggs per day is used to compensate mortality during winter. The peak of the laying rate (2000 eggs per day) is the same as used by *D.S. Khoury et al.* [1] and *Wright* [8]. The results are discussed in chapters 5.1 and 5.2 with the corresponding plots in appendix A.1.2 and A.1.3.

$$\frac{dB}{dt} = L_t S(H, f) - \varphi B \quad (7)$$

The introduction of dynamic laying rates led to problems with the mortality rates tested by *D.S. Khoury et al.* [1]. We discuss this in chapter 5.2.

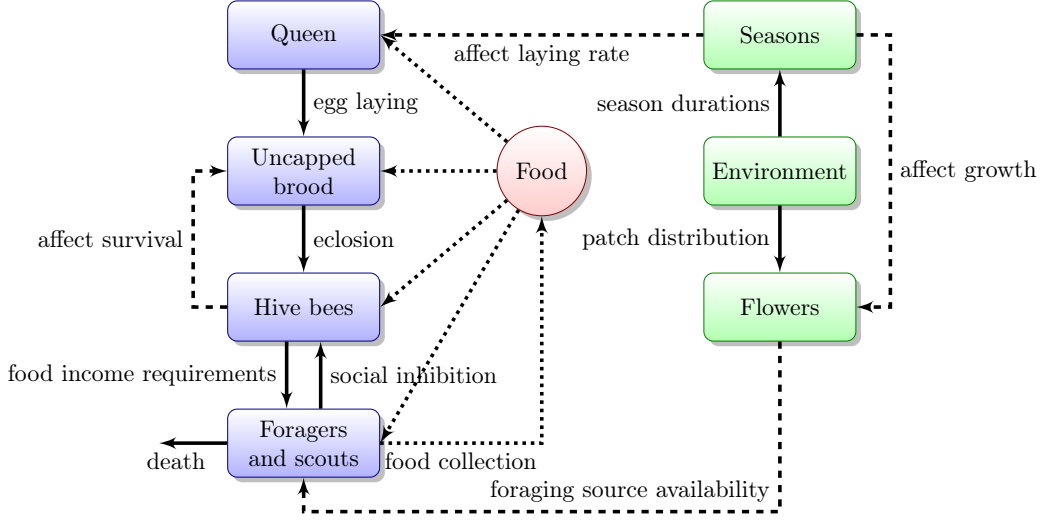


Figure 2: *Honey bee social dynamics and environmental influences covered by our advanced model.*

### 3.3 Advanced model: Environment simulation

As we were interested in observing the social dynamics under different food availability conditions, in contrast to the model of *D.S. Khoury et al.* [1], we had to implement a simulation for the environment. This advanced model introduces an environment with seasons which affect the queen’s laying rate (see equation 7), the distribution and quality of flower patches and seasonal flower growth. The forager bees are then simulated in this environment, searching and collecting food according to the rules in chapter 3.3.1. An overview of the complete model is given in Figure 2.

Note that the environment simulation is triggered for day  $t$  after the basic model has computed all differential equations for day  $t - 1$ . If there is no flower blooming on day  $t$ , we assume the daily food income  $f_{d,t} = 0$  (see equation 11) and skip the environment simulation for this day.

#### 3.3.1 Bees’ working states

The environment simulation only simulates forager and scout bees. Hive bees are not considered as agents. For the foragers and scouts, we developed a set of simple rules which try to be as close as possible to the foraging process described by *T.D. Seeley* [2]. All essential rules are represented in Figure 3.

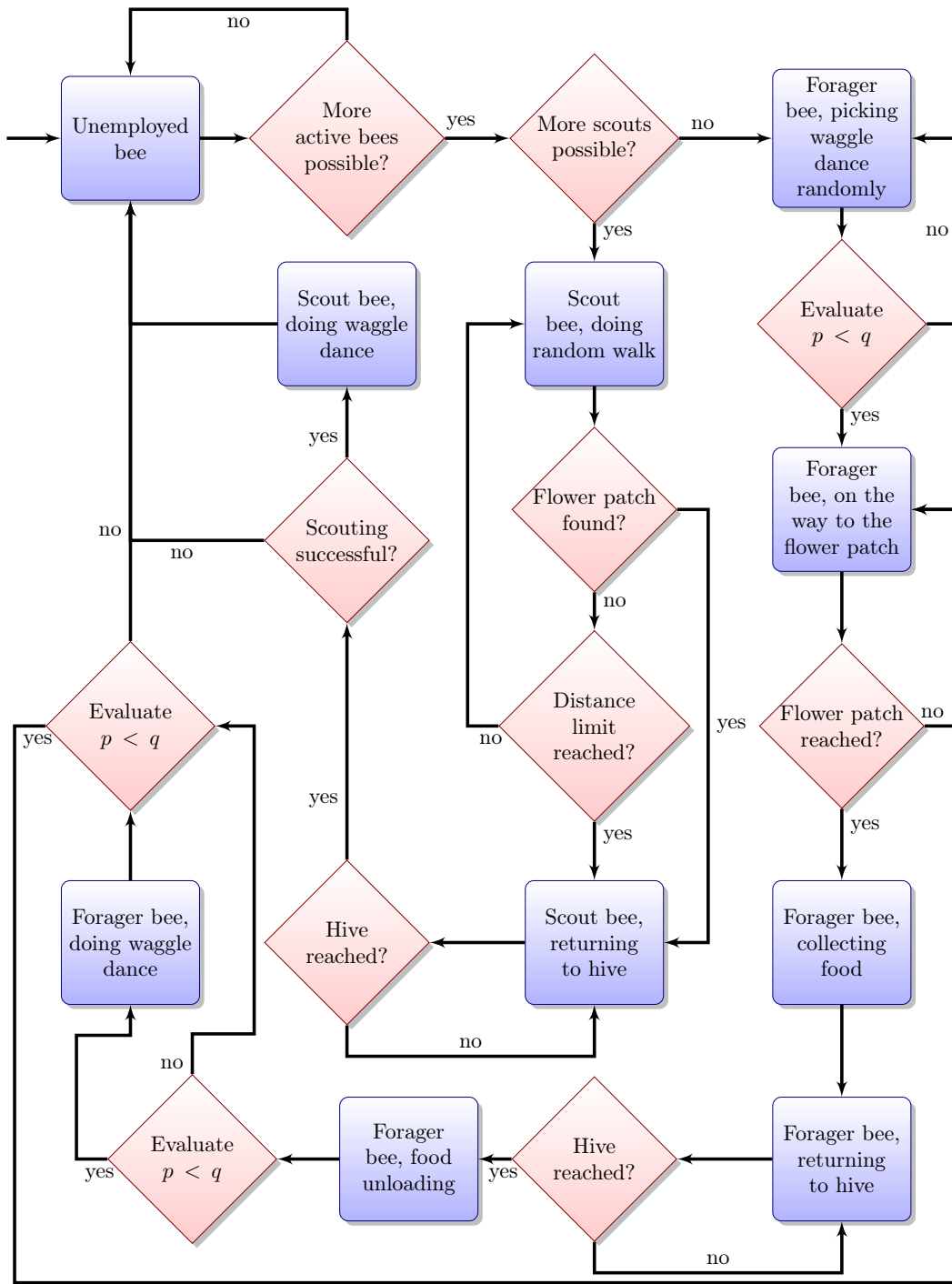


Figure 3: *State transitions of the bees in the environmental simulation.*

At the beginning of every day ( $t_s = 0$ ), all bees are unemployed. There are three possibilities for every unemployed bee which are considered in every simulation step:

- If the amount of active bees according to the current time of the day is not reached, the bee can get a job assigned. Otherwise the bee stays unemployed.
- If the maxima of scouts is not reached (6% of the bees' foragers [2], p. 86), then the bee becomes a scout.
- Otherwise, the bee becomes a forager.

When a bee agent gets a scouting job assigned, the agent continues the following way:

- The scout performs a random walk (see chapter 4.3.1) and checks with every iteration step, if any flower patch has been passed (see chapter 4.3.2).
- If a flower patch is found or the flight distance limit is reached, the bee returns to the hive. Path optimization (see chapter 4.4.1) may occur.
- Back in the hive, the bee performs a waggle dance if scouting has been successful and goes back to the unemployed state.

When a bee agent gets a foraging job assigned, the agent continues the following way:

- Among the available waggle dances, the forager chooses randomly and evaluates if the food source is good enough ( $p < q$ ) to visit or not (see chapter 3.3.2). This is repeated in every iteration step until the forager decides to visit the flower patch represented by the chosen waggle dance.
- The forager flies to the patch and, upon reaching it, collects as much food as the flowers in the patch allow (see chapter 3.3.3).
- After foraging, the bee returns to the hive. Path optimization may occur again.
- Back in the hive, the forager unloads the collected food (increasing  $f_{d,t}$ , see equations 10 and 11).
- The bee now has to evaluate the food source several times ( $(p < q)$ , once per iteration step) and decide if it is worth reporting the patch (performing a waggle dance) or not.
- A final evaluation ( $p < q$ ) has to be done to decide if the forager will abandon it's own food source and become unemployed or fly to the same patch again.

### 3.3.2 Foragers' distribution across flower patches

It is clear from chapter 3.3.1 that after some time, the bees will focus on newly reported and then on the most profitable food sources because of the relative quality evaluation.  $p \in [0, 1]$  denotes an equally distributed random value.  $q$  denotes the relative quality of a given flower patch compared to all patches currently available as a waggle dance. In detail, the evaluation ( $p < q$ ) works as follows:

At the beginning of every iteration step, the waggle count  $n_w$  is set to zero. Every bee that does a waggle dance at the moment then writes the flower quality  $b_w$ , distance to the flower patch  $d_w$  and size of the patch  $A_w$  into the corresponding vector. This gives three vectors:

$$\begin{pmatrix} b_{w,1} \\ b_{w,2} \\ \dots \\ b_{w,n_w} \end{pmatrix} \quad \begin{pmatrix} d_{w,1} \\ d_{w,2} \\ \dots \\ d_{w,n_w} \end{pmatrix} \quad \begin{pmatrix} A_{w,1} \\ A_{w,2} \\ \dots \\ A_{w,n_w} \end{pmatrix}$$

To compare a (potential) waggle dance with given  $b_w$ ,  $d_w$  and  $A_w$  against the existing ones, the following formula is used:

$$q_w = b_w \cdot \max\left(\begin{pmatrix} b_{w,1} \\ b_{w,2} \\ \dots \\ b_{w,n_w} \end{pmatrix}\right)^{-1} \cdot d_w \cdot \max\left(\begin{pmatrix} d_{w,1} \\ d_{w,2} \\ \dots \\ d_{w,n_w} \end{pmatrix}\right)^{-1} \cdot A_w \cdot \max\left(\begin{pmatrix} A_{w,1} \\ A_{w,2} \\ \dots \\ A_{w,n_w} \end{pmatrix}\right)^{-1} \quad (8)$$

We update and obtain a fourth vector, every time a new waggle dance is executed, keeping track of all relative patch qualities. Every time a bee decides to do a waggle dance in the current iteration step, the update is computed:

$$\begin{pmatrix} q_{w,1} \\ q_{w,2} \\ \dots \\ q_{w,n_w} \\ q_{w,n_w+1} \end{pmatrix} = \begin{pmatrix} q_{w,1} \\ q_{w,2} \\ \dots \\ q_{w,n_w} \\ q_w \end{pmatrix} \cdot \max\left(\begin{pmatrix} q_{w,1} \\ q_{w,2} \\ \dots \\ q_{w,n_w} \end{pmatrix}, q_w\right)^{-1} \quad (9)$$

Obviously, if the new patch is the best one,  $q_w > 1$  holds, otherwise  $q_w \in (0, 1]$ . In the first case there will always be a waggle dance propagating this patch. Otherwise, it depends on how the bee chooses randomly  $p \in [0, 1]$  and then if  $p < q_w$  holds. The same evaluation happens when a bee has to decide on giving up a patch or after watching a waggle dance (see fig. 3).

Of course, on the implementation side, we have to keep track of which vector index

$i \in \{1, 2, \dots, n_w\}$  belongs to which path element. The path a bee chooses is copied to the bee's memory.

A path for a certain patch can get smaller by optimization (see chapter 4.4.1), thus the patch can obtain a better relative quality  $q_w$ . This will lead to higher propagation probability for the same patch. This means more bees will (over time) take the shorter path to any given flower patch, either by optimizing themselves or by looking at waggle dances of patches with shorter paths.

The question arises, how bees can have such deep knowledge of the own patch and the quality of patches represented by waggle dances. *T.D. Seeley* [2] gives insight and assumptions on this matter. In chapter 5.4., p. 92, he states that bees can use dance duration, frequency and variation to communicate patch profitability. This indicates our model is a useful approximation in terms of waggle dance/path sharing. In chapter 5.5 he writes that travel distance and expected profit are the driving factors in determining patch quality. We also added the patch size  $A_w$  in our model, as it is also a profit indicator when looking at the patch on a larger scale. The last question is if bees have preprogrammed knowledge what a good and a bad flower patch is or if this is a relative question depending on daily situations. We assumed the second one and *T.D. Seeley* confirms this in chapter 5.7. on p. 104: For food unloading, hive bees prefer to unload the most profitable income first. This means, bees with a bad flower patch have to wait longer, telling them their choice was probably not the best. Waiting times may vary randomly, thus adding randomness to the evaluations ( $p < q$ , fig. 3) makes sense as well.

### 3.3.3 Food collection

With every flight, a bee can gather  $f_b = \min(f_{p,t}, f_{b,max})$  grams of pollen and nectar, where  $f_{b,max}$  is the physical top limit of the bee.  $f_{p,t}$  (the reward of a certain patch) is derived from  $f_{b,f}$  (see chapter 3.4.2) by multiplying  $\max(f_{b,f})$  with the growing quality of a certain patch on day  $t$ , denoted  $b_w \in (0, 1]$ . Note that  $b_w$  itself is derived from the map (see chapter 4.2) and the normalized  $\frac{f_{b,f}}{\max(f_{b,f})}$ . The daily food sum is increased every time a forager bee reaches the hive:

$$f_{d,t} = f_{d,t} + f_b \cdot F_{b,t} = f_{d,t} + \min(\max(f_{b,f}) \cdot b_w, f_{b,max}) \cdot F_{b,t} \quad (10)$$

An additional factor  $F_{b,t}$  is used for clustering. This means we only simulate up to  $\frac{F}{F_{b,t}}$  actual agents on day  $t$  and then interpolate to the actual value, which saves a lot of computation time. For relatively small cluster sizes, respectively, many actual agents (in the order of 1000), the variation of  $f_{d,t}$  will be small because the mean value

of bees visiting a patch over a whole day is about the same as without clustering, according to the law of large numbers (LLN).

Finally, we obtain a new equation to replace the original equation 6 for the daily food change:

$$\frac{df}{dt} = f_{d,t} - \gamma_A(F + H) - \gamma_B B \quad (11)$$

where  $f_{d,t}$  denotes the amount of food the foragers collected on day  $t$ .

We discuss the numerical results of this model in chapter 5.3.

### 3.4 Empirical data bases

#### 3.4.1 Area around the hive

By analysing the different waggle dances of the forager bees, *T.D. Seeley* states in *Wisdom of the Hive* pp. 37ff., that 95% of the foraging process occurs in a radius of 6.0 km (maximum distance at 10.9 km, mean distance at 2.2 km and the modal distance at 1.6 km [2]). The approximation of our modelled square  $(6 \text{ km} \cdot 2)^2 \approx 100 \text{ km}^2$  should be sufficient for the simulation and comprehend all important data. In our model, we split the area up into a grid of 10 m · 10 m tiles of flower patches.

#### 3.4.2 Flower patches and food

The flower patches themselves are divided into their different blossom: spring, summer and autumn. The empirical data was taken from *Wisdom of the Hive* pp. 44f.: Year 1982 from Figure 2.14 was combined with the data from Figure 15.2 (representing the significant months of weight gain) and we received a new graph for the whole year (see fig. 4). With equation 12, we can find out the weight of food a bee carries per flight.

$$f_{b,f} \left[ \frac{g}{\text{flight and bee}} \right] = \frac{M \left[ \frac{kg}{\text{day}} \right]}{C [\text{bees}] \cdot l \left[ \frac{\text{flights}}{\text{day and bee}} \right]} \cdot 1000 \left[ \frac{g}{kg} \right] \quad (12)$$

The result  $f_{b,f}$  is an approximation in gram per bee and flight.  $M$  denotes the change of the mass of the hive per day in kilograms (see fig. 4) and  $C$  represents the forager bee count approximated for a specific day of *T.D. Seeley's* empirical data [2].  $l$  denotes the number of flights a bee can perform on average per day. Thus, we can take hive weight change per day as an indicator for the flower quality and flower type present at a given day of the year. This is the best approximation we tried; unfortunately, we did not find any actual data of blooming and foraging profit, as it is very difficult to measure this in nature quantitatively.



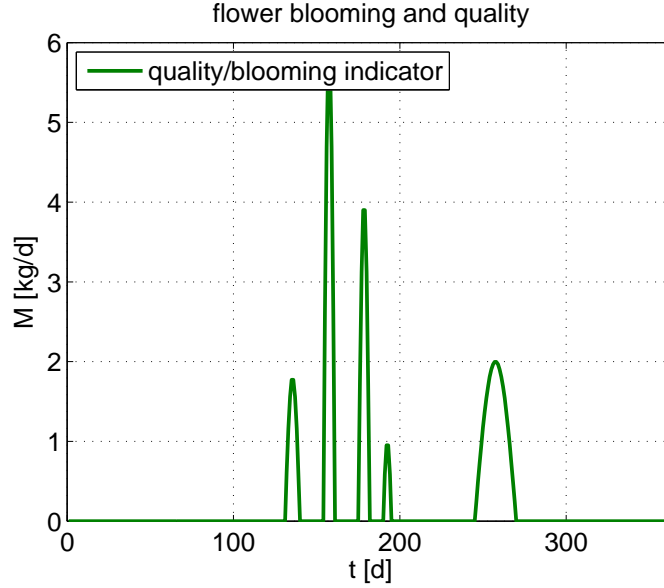


Figure 4: This figure shows the change of the mass of the hive for any day in the year. It correlates with the quality of a flower patch and the type of flower, respectively.

### 3.4.3 Bees' parameter

The data about number of bees are fully based on *D.S. Khoury's* model [1]. He used 16 000 hive bees and 8 000 forager bees, which seems to be the right order of magnitude and is congruent with *T.D. Seeley's* estimation of about 20 000 [2].

The food consumption for adult bees (0.007 g) and brood (0.018 g) was taken from *J. R. Harbo's* works [9].

As remarked at the beginning of chapter 3.1, we simplify the complicated ageing process (larvae to hive bee) to 12 days without further distinction between eggs, larvae or pupae. Mortality rate is set to 0.075 and thus slightly lower than the values of *D.S. Khoury*. This is discussed later in section 5.2.

$f = 50\,000$  corresponds to 50 000 g of initial food storage. The parameter for the adult bee emerging factor  $\varphi = \frac{1}{9}$  is an assumption and was adopted from *D.S. Khoury's* paper, as well as  $v$ ,  $b$  and the recruitment factor  $\alpha = 0.25$  (see chapter 3.1). Those values are empirically tested but not explained any further.

## 4 Implementation

### 4.1 General implementation

The basic simulation consists only of the evaluation of the equations for every time step. The implementation can be found in the *Hive.m* code. Variable names are chosen so that they match *Khoury et al.* [1] and chapter 3.1 as close as possible.

For the advanced model, the following hierarchy is used: The top level is the *hive\_simulation.m* file, which sets up the whole simulation. Then it keeps track of data and iterates through days in the hive simulation and through seconds in the environment simulation. The *Prop* class (*Properties\_Base.m*) is an implicit struct which allows to plug in and change empirical data and simulation parameters. For the environment simulation, *Bee* (*Bee.m*) is the class for agents, *Hive* (*Hive.m*) for hives and *World* (*World.m*) for the maps.

The final report (simulation results) is stored as class *Report* (*Report.m*) with an implicit struct, making data analysis easy and extendible.

### 4.2 Map and flower patch quality

The bees all navigate on a map with the hive in the middle of the map. Every pixel on the map equals to a patch of 100 m<sup>2</sup>.

The map is encoded in HSV (see fig. 5). From the 360° color hue circle ( $H_{HSV} \in \{0, 1, \dots, 360\}$ ), always 60° are assigned to one integer type value  $j \in \{0, \dots, 5\}$ . Value 0 is used for empty space and values 1 to 3 for the three flower seasons/types we implemented. Values 4 and 5 are for future extensions such as smog/pesticide sources. More values can be gained by assigning less than 60° per type. The saturation  $S_{HSV} \in [0, 1]$  is always kept at 1. For the flower patch quality basis, the brightness value  $V_{HSV} \in [0, 1]$  is used.



Figure 5: Map encoding in HSV.

To obtain the daily map for environment simulation, the normalized blooming indicator (see fig. 4) of each flower type  $i \in \{1, 2, 3\}$  is separately multiplied with the

$V_{HSV}$  value of the basis map where flower type  $i$  occurs (see fig. 6). As a result, some flowers don't appear on the map and those that appear get scaled in quality according to the daily situation (see fig. 2). From the obtained scaled quality map, the bees now read the value  $b_w$  when visiting a patch. This is the driving factor for forager distribution (see chapter 3.3.2).

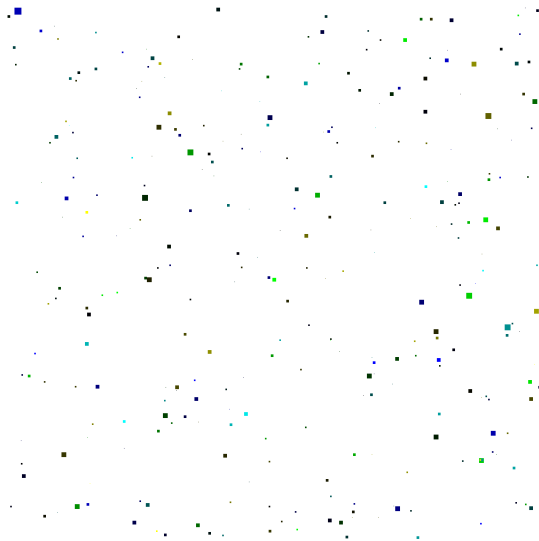


Figure 6: *Example of an equally distributed flower patch, normally distributed quality map. Note that the encoding is given by Figure 5 but background black has been swapped out with white for better visibility.*

### 4.3 Scouts

#### 4.3.1 Random walk

Very little is known about the searching behaviour of scout bees [2], p. 87f. *T.D. Seeley* mentions that scouts fly low above the ground and inspect flowers they encounter during their flight. Naturally, the flight distance is limited. Considering this, a random walk is the most logical behaviour to simulate scout bees. The random walk is stopped when a scout encounters a new flower. Previously discovered flower patches are ignored by scouts, as bees mark already visited patches with the *Nasonov pheromone* [10] p. 133ff.

The random walk is performed in following steps:

- The bee starts from the hive with an equally distributed random angle  $\alpha \in [0, 2 \cdot \pi]$  (radian).

- After a number of time steps (we have chosen one time step, so 60 seconds), the angle  $\alpha$  is changed by at most  $r \cdot 0.5$  (radical angle changes are not desired), where  $r$  is a normally distributed random value.
- Between two angle changes, the scout bee flies with 7 m/s into the chosen direction.
- The path points are recorded at every angle change point. The distance passed is calculated and stored in a  $L^2$  norm scalar.

The path a scout bee walks is recorded in a vector of  $x$  and  $y$  coordinates:

$$\begin{pmatrix} x_0 & x_1 & \dots & x_n \\ y_0 & y_1 & \dots & y_n \end{pmatrix}$$

where  $\begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$  are the hive coordinates and  $\begin{pmatrix} x_n \\ y_n \end{pmatrix}$  are either the coordinates with maximum possible distance from the hive according to  $L^2$  norm, or the coordinates of a flower patch.

An example of such a random walk is given in Figure 7.

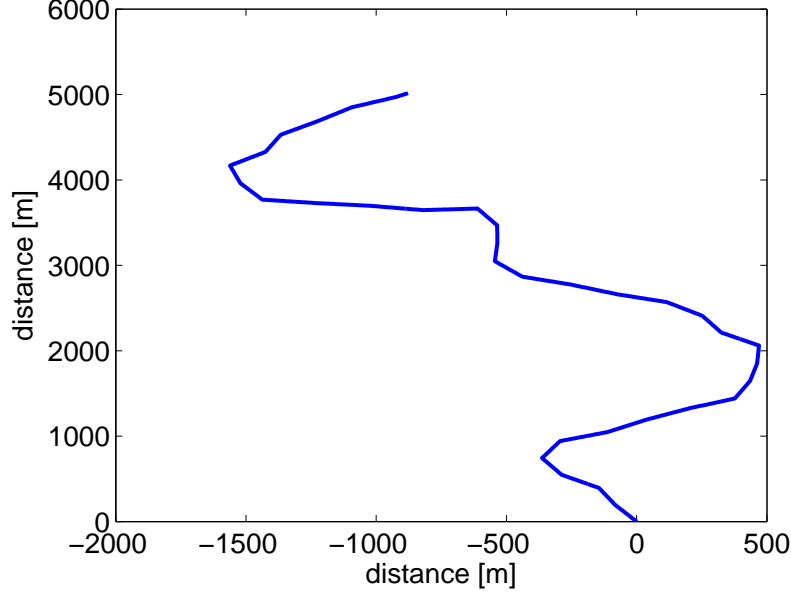


Figure 7: *Example of a random walk executed by a scout bee.*

### 4.3.2 Bresenham line algorithm

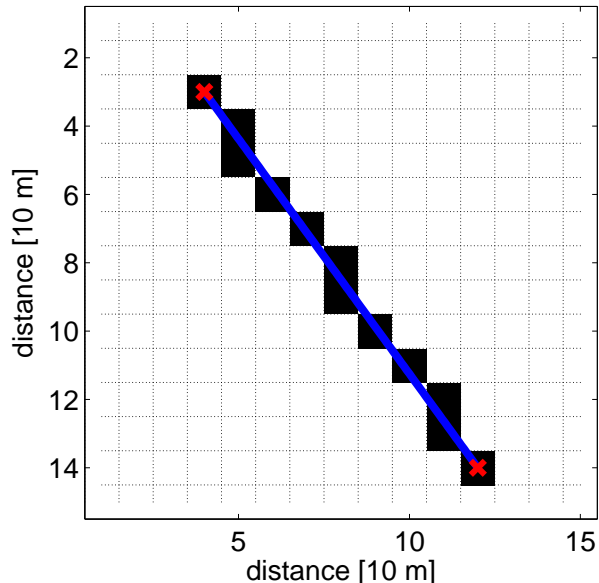


Figure 8: *Example of Bresenham's line algorithm with map and path segment.*

As the scout bees pass a distance of  $v \cdot \Delta t_s$ , respectively  $\sqrt{(v_x \cdot \Delta t_s)^2 + (v_y \cdot \Delta t_s)^2}$  for a velocity  $v$  and time step  $\Delta t_s$  in every iteration step, multiple fields are being passed at once. In order to check all fields between the last and current iteration step for flower patches, the Bresenham line algorithm is used. With this method, all integer coordinates between two given points on the map are reported back. Afterwards, every obtained point can be checked against the current quality- and type-map of the environment simulation. For this simple algorithm, a pre-existing implementation is used [11]. Figure 8 is an example on a 15x15 map with coordinates  $(x = 4, y = 3)$  to  $(x = 12, y = 14)$  and reported points (black boxes).

## 4.4 Foragers

### 4.4.1 Path optimization

We assume bees can optimize the original path they obtain from a waggle dance, as the bees are able to orientate themselves in the environment with sun positioning [2], p. 37. The implementation used is a simple one, in order to keep computation times low. At every point where optimization may occur (see chapter 3.3.1), there

is a 50% chance of optimization. Optimization works as follows:

$$\begin{pmatrix} x_0 & x_1 & x_2 & x_3 & x_4 & \dots & x_{n-3} & x_{n-2} & x_{n-1} & x_n \\ y_0 & y_1 & y_2 & y_3 & y_4 & \dots & y_{n-3} & y_{n-2} & y_{n-1} & y_n \end{pmatrix} \Rightarrow_{\text{optimization}} \begin{pmatrix} x_0 & x_2 & x_4 & \dots & x_{n-4} & x_{n-2} & x_n \\ y_0 & y_2 & y_4 & \dots & y_{n-4} & y_{n-2} & y_n \end{pmatrix}$$

This means every second way point is skipped, while starting- and endpoints are preserved. According to the triangle inequality, the  $L^2$  norm of the distance can only become smaller after every such step, therefore it is an optimization in terms of path length. The outcome of such an optimization process on the path from Figure 7 is presented in Figure 9.

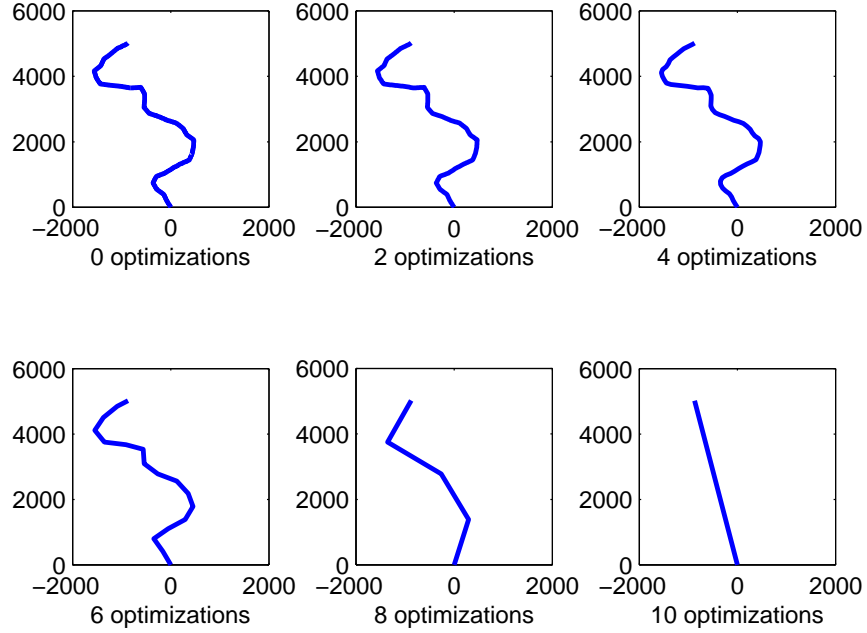


Figure 9: *Example of path optimization used to short cut the path to flower patches.*

Comparing this model of optimization with empirical observations made by *Lihoreau et. al* [12], p. 3, shows that our model is a good approximation: They state that the bees reduce their travel times gradually with experience and higher numbers of flights. The same happens in our model, as the shortest path is not taken directly,

but shorter paths are taken after visiting a certain patch often enough. The only difference is that we don't explicitly simulate multi-patch sequences (bees can visit multiple patches before returning to the hive) while *Lihoreau et. al* primarily focus on this matter.

## 5 Simulation Results and Discussion

### 5.1 Constant food and egg laying

The first iterative simulation run is based only on the equations of *David S. Khoury et al.* [1]. As expected the hive stabilizes at an equilibrium point while the stored food increases infinitely (see fig. A.1.2).

### 5.2 Constant food, dynamic egg laying

In the second iterative simulation run we wanted to see, if the new laying function (see fig. 1) was working as intended. As a result, the bee population does not stabilize at one point, but describes now a more natural, periodic form with a population maximum around August and a minimum around February.

The colony we simulated did not survive with any daily mortality rates greater than 0.1. There are not enough bees emerging from the pupa stadium to compensate the mortality rate. However, we found that the new mortality rates assumed in our simulation (0.075 daily mortality) are still realistic. *Henry et al.* [13] describe mortality rates between 0.102 and 0.316 in empirical testing, which is the range in which *Khoury et al.* [1] simulated. *R. Dukas* [14] observed that mortality of foragers mainly occurs in this range because of predation. Since we apply the mortality to all days, even in times and seasons without foraging (all bees stay in the hive), our simulated mortality rates are naturally lower.

The stored food still increases infinitely, as the everyday income per forager bee is constant (see fig. A.1.3).

### 5.3 Environmental model

To test the environmental model, we decided to change the quality indicator and delay seasons (especially autumn). The map (see chapter 4.2) is always randomly generated with equally distributed flower patches on it and normally distributed flower patch quality. All other parameters are kept constant to obtain unambiguous results.

## 5.4 Empirical data based runs

In this set of simulation runs we wanted to see if our model can produce the same results as *T.D. Seeley's* experiments from *Wisdom of the Hive* p. 44, Figure 2.14, year 1982. Our graphs in A.2.2 correlate well with the empirical data (before a swarm leaves the hive). As swarming was never a part of our model, we were satisfied with the accuracy of the results. Furthermore, we could compare the graphs only visually, since *T.D. Seeley* did not publish any extensive numerical data of his empirical evidence.

Compared to our earlier simulations, the food collection rate is now dominated by the availability of flowers and the forager count.

### 5.4.1 Typical simulated day (environment interaction)

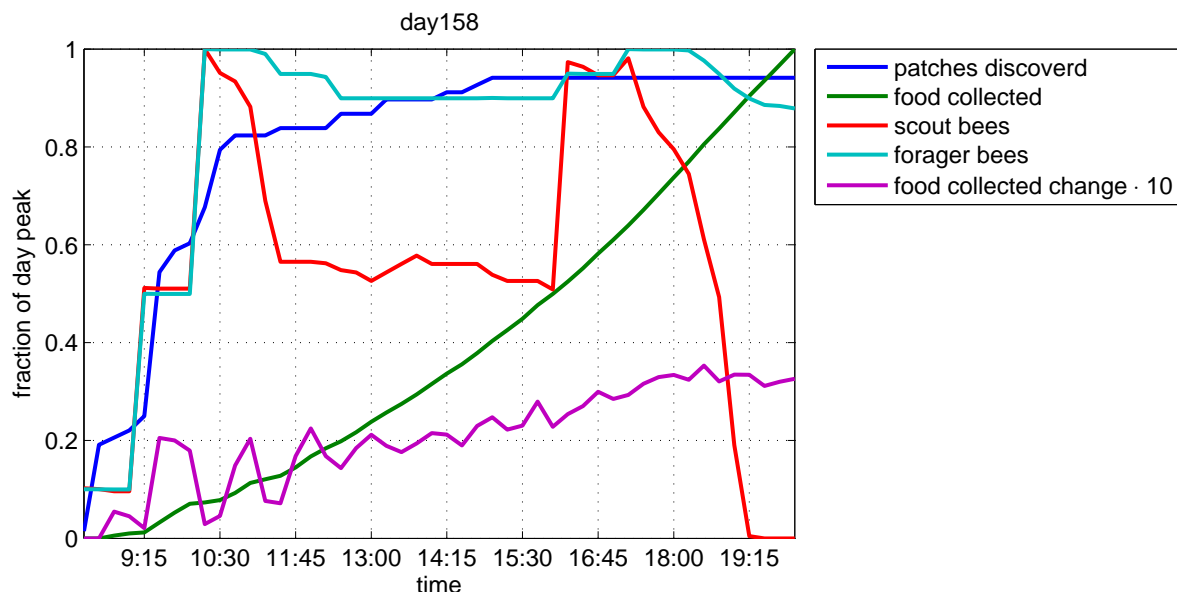


Figure 10: A summer day (day 158) from the standard run A.2.2. Values are given in fraction of the maximum value reached on day 158.

The analysed day number 158 represents a peak in summer flower blooming, so we can easily extract some information. On a typical summer day like this, the scout bees discover about 80% of the patches after 2.5 hours. The rate at which the food is collected is increasing throughout the day, which is represented by the *food collected change* graph in Figure 10. We attribute the fluctuating changes in the first 4 hours



to the discovery of new patches and the first path optimizations taking effect. The change of collected food stabilizes as the path optimization has run its course and no new food sources are discovered (see fig. 10).

For the statistical analysis of this summer day, we've averaged the values and calculated the standard deviations for every parameter captured during an environment simulation (see fig. 11). The 20 runs needed for chapter 5.4.3 were used as data basis. For spring and autumn, the plots would look approximately the same because an equally distributed flower map is used. This means the same optimizations and scouting behaviours are expected.

High correlation can be found between the amount of discovered patches and the slope/change of food income (linear correlation coefficient of 0.9263). This was expected because with a higher count of discovered patches, bees are able to figure out the best ones and increase their income.

A little less, but still significantly correlated is the amount of active foragers to food income (linear correlation coefficient of 0.8767). The least significant correlation is found between active scouts and food income (linear correlation coefficient of 0.5076). This makes sense since scouts are not collecting food, only discovering flower patches. In Figure 10 and 11, the number of scouts and foragers decreases a bit by the middle of the day, between 10:30 and 16:30. The food income change directly reacts to this. This change in active bees exists because we selected the daily activity curve of the bees this way, according to *T.D. Seeley's* empirical data (*Wisdom of the Hive*, p. 86, fig. 5.2. [2]).

The standard deviations are not significant for the discovered flower patches because with the high amount of scouts on this particular day (about 6% of 20 000 bees), most of the introduced randomness is compensated (for random walk, see chapter 4.3.1).

The number of active scouts and foragers varies a little, but mainly follows the activity curve we've chosen. The deviation is higher for scouts than for foragers because the amount of scouts is about 20 times smaller while the introduced variations happen in an absolute way (the balance between scouts and foragers can vary between two runs).

Food income change has the highest deviation values because this is strongly dependent on the bees' selection of waggle dances (see chapter 3.3.2). However, over the day, the deviation becomes smaller because bees always optimize towards the highest food income. This is also reflected in the total food collected over the day: At the beginning, we observe low deviations. The highest values are found on the middle of the day. At the end of the simulated day, the deviation is close to non-existent.

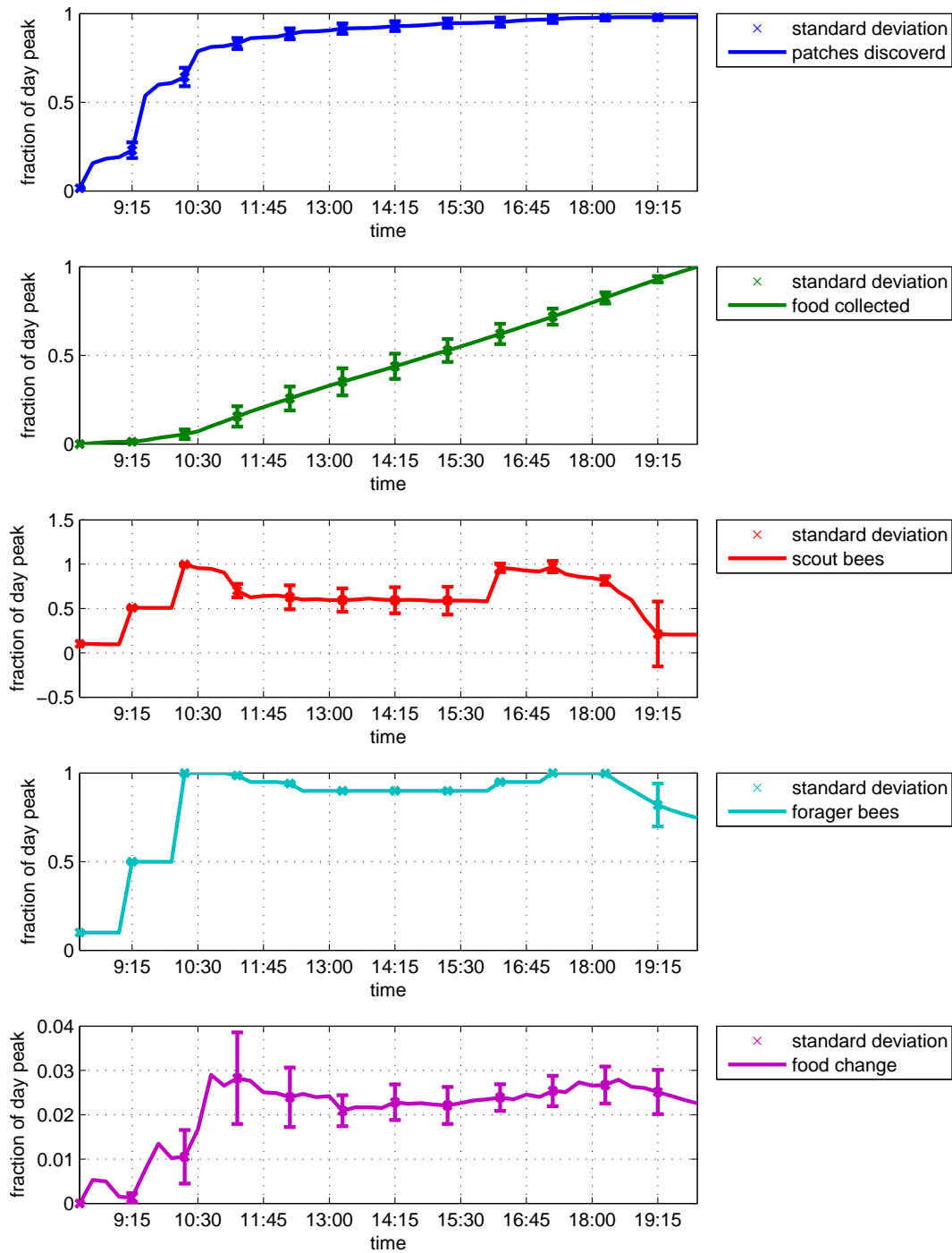


Figure 11: A summer day (day 158), mean values over 20 runs from the standard run shown in appendix A.3 with deviations. Values are given in fraction of the maximum value reached on day 158.

### 5.4.2 Missing flower seasons

In our first set of simulations (see A.2) we tested if any of the simulated blooming periods is not vital to the hive. We wanted to analyse the compensation mechanism of the hive and how the basic model interacts with the environmental simulation.

When removing the spring blossom (see A.2.3) from our simulation, we discovered that it did not necessarily lead to a critical situation in terms of food. However, the peaks of the stored food in summer were lower than those from the standard run A.2.2. We trace this back to the bee's ability to compensate the missing food income by consuming their stored food until summer.

On the other hand, if summer or autumn are left out, the hive collapses. In the first case, the bees will survive the summer but the hive population dwindles to a level of about 1000 bees (see A.2.4). This is not sufficient to collect enough food in autumn and the hive dies. On day 200 (after all stored food is consumed) something very interesting happens: In order to survive, the bees stop taking care of the brood and eventually eat up the larvae (see equation 2, chapter 3.1). Because of the high need to get food, equation 5 of the basic model tries to recruit foragers from hive bees. From there on, both hive bee and forager population decreases as there is no brood to compensate mortality. On day 250, when the autumn season begins, not enough foragers are available and food, brood and bee numbers decrease monotonically.

In case of a missing autumn food income (see A.2.5), the hive will starve as the bees consume the whole stored food before winter really begins. Again, the bees try to compensate by assigning more foragers, which doesn't help and would be counterproductive in a real world scenario (higher mortality of foragers and energy loss due to pointless foraging). By cannibalizing their brood, bees can help themselves through a short term lack of food (slightly delayed seasons or bad weather) but not through a whole missing season.

### 5.4.3 Variations of autumnal flowers

The idea behind variations of autumn flowers was to see at which delay or quality reduction the hive would start to collapse. For the quality indicator, we tested values between peak  $M = 2.0 \frac{kg}{day}$  and  $M = 0.5 \frac{kg}{day}$  (in steps of 0.5) for the autumn flowers (see fig. 4 and chapter 3.4.2). We delayed the season between 4 and 20 days (in steps of 4 days). More delay would shift the flowers into late autumn and winter, which makes no sense.

We used 20 000 g and 1000 bees as the minimal requirement needed to survive in mid-

winter. These values were chosen in accordance with observations from the graph shown in appendix A.2.2: About 20 000 g of food is consumed from January to May to stabilize the hive and start brood reproduction to be ready for next summer's foraging. With less than 1000 bees, the hive can not fire up reproduction fast and reliable enough (see equation 2 and chapter 3.1.)

We found, that shifting the season by those 16 days has no significant effect on the forager count. Thereby the overall food gathering potential of the hive is not reduced enough to cause problems. But a decrease in flower blooming quality reduces the amount of food to be gathered regardless of the forager bee count. Consequently, with  $M = 0.5 \frac{kg}{day}$  (see appendices A.3.11 to A.3.13), the hive can not survive. The minimal stability point is around  $M = 1 \frac{kg}{day}$  (see appendices A.3.8 to A.3.10). At this point, the deviation of collected food over the year (see fig. 12) becomes significant enough (3 to 5 kg) to affect the survival.

Note that the standard deviation in Figure 12 basically derives from the environment simulation (daily standard deviation of food income, see fig. 11). Therefore it only increases on foraging days, not during days without foraging and does not decrease.

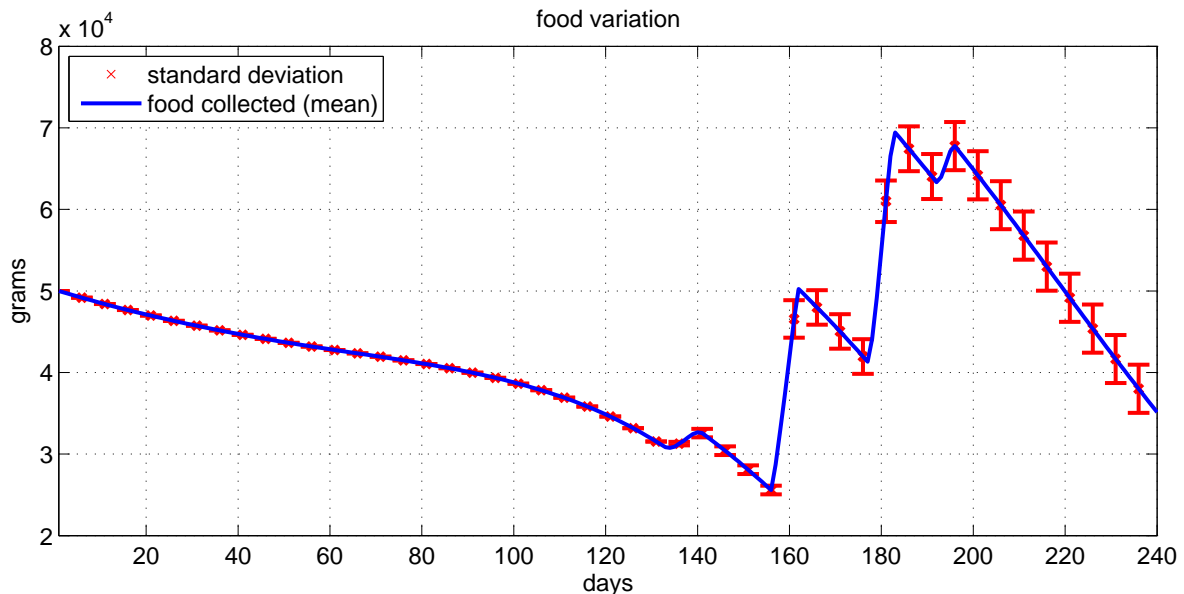


Figure 12: Food variation from January to August, mean values over 20 runs from the second set of simulation runs in appendix A.3.

#### 5.4.4 Model restrictions

Even though we extended *Khoury's* model by environmental influences on flowers and food reward, it is far from complete. One big divergence from nature is the treatment of pollen and nectar as one. Pollen, which is the protein source, and nectar, which is the carbohydrate source, are actually collected by two different forager classes intracolonially [15].

Another big source of disturbance are diseases, infections, predation and swarming. Impairments in different aspects of a bee's life and behaviour, caused by pesticides or genetic mutation are entirely left out. There are also no other environmental influences such as aridity, wetland or weather and no human influences.

In the end, one has to simulate the bee's way of "thinking", which is still a long way to go or might never be fully understood.

## 6 Summary and Outlook

### 6.1 Realistic flowers and maps

To increase the accuracy of our model further, the flower blooming functions could be split up more minutely. They could be replaced by more accurate quantitative relations, than those we used. Moreover, flower distribution was computer generated; it would be very interesting to create maps of real places (agricultural areas vs. urban and suburban areas, maps near heavily used roads etc.) and compare their results.

### 6.2 Improvements to the hive model

The model would actually support multiple hives with different parameters. For example, various bee species could be simulated on the same map contesting for food.

Furthermore, we never tried to implement swarming in our model. With the model's ability to handle multiple hives one could implement swarming and find out more about the evolution of bee hives and their long term behaviour.

Some of our measures to reduce run-time (clustering, bigger time steps) could be reversed to increase the model's accuracy (runtime can go up to 10 hours for a simulated year with the most precise settings (as of 2013)).

### 6.3 Summary

Overall we found that bees can compensate short term food problems quite well by sacrificing larvae and recruiting bees for the most important tasks. They can not compensate however, the loss of a whole season (e.g. summer or fall) or a substandard

flower blooming in summer or fall.

Interestingly enough, most of our calculated and simulated data correlate nicely with the literature of our two basis papers (*Khoury et al.* [1] and *T.D. Seeley* [2]), even though we took values from many different sources.

## 6.4 Outlook

In our rapidly developing world, studies like this become more and more important. Things like bees, seemingly 'unnecessary' insects, have a very big influence on our way of life - and vice versa. It is intriguing to see, how a simple model, compared to nature, can predict events so precisely and so fallaciously at the same time. Models are always extensible and improvable, which is exactly what should be done. Only with science, we can find out more about the world.

## 7 References

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## A Additional Graphics

### A.1 Simulation run without environment simulation

#### A.1.1 Runscript with changes relative to the base properties

```
% This is a runscript for automatized simulation on any system

% Simple test cases based on Properties_Base
run('data\Properties_Base.m');

% Load the properties into memory, make copies and modify them on the go

% The testcases:
% 1. Original model (constant food, constant laying rate, original mortality)
% 2. Intermediate model (constant food, varying laying rate, adapted mortality)

Prop1 = Prop;
Prop1.Sim.Hive(1).fixed_food_rate = 1;
Prop1.Sim.Hive(1).mortality = 0.3;
Prop1.Sim.Hive(1).laying_function = [0,1,2;1,1,1];
Prop1.Sys.identifier = 'Properties_Base_R0_1';

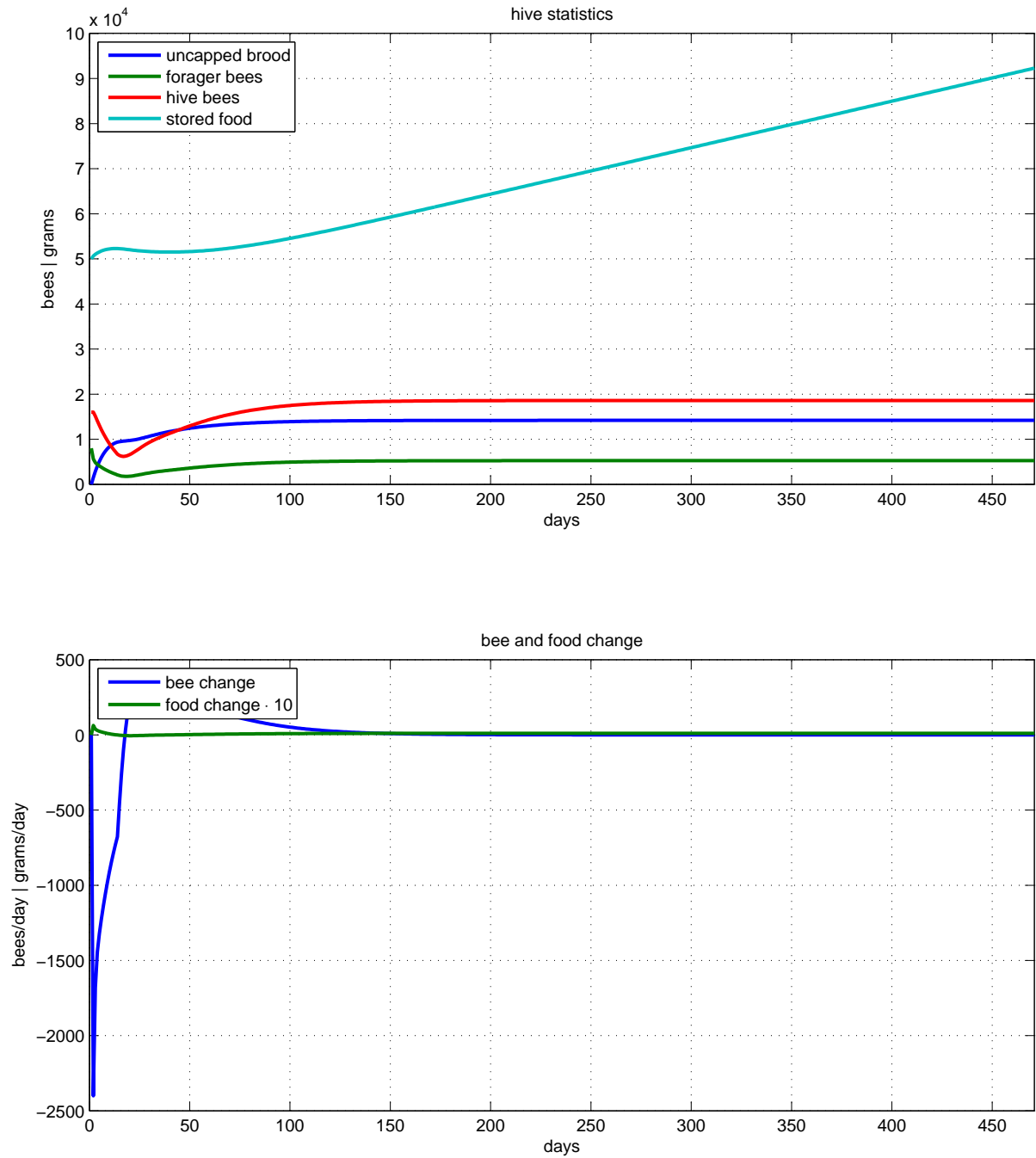
Prop2 = Prop;
Prop2.Sim.Hive(1).fixed_food_rate = 1;
Prop2.Sys.identifier = 'Properties_Base_R0_2';

proparray=[Prop1,Prop2];

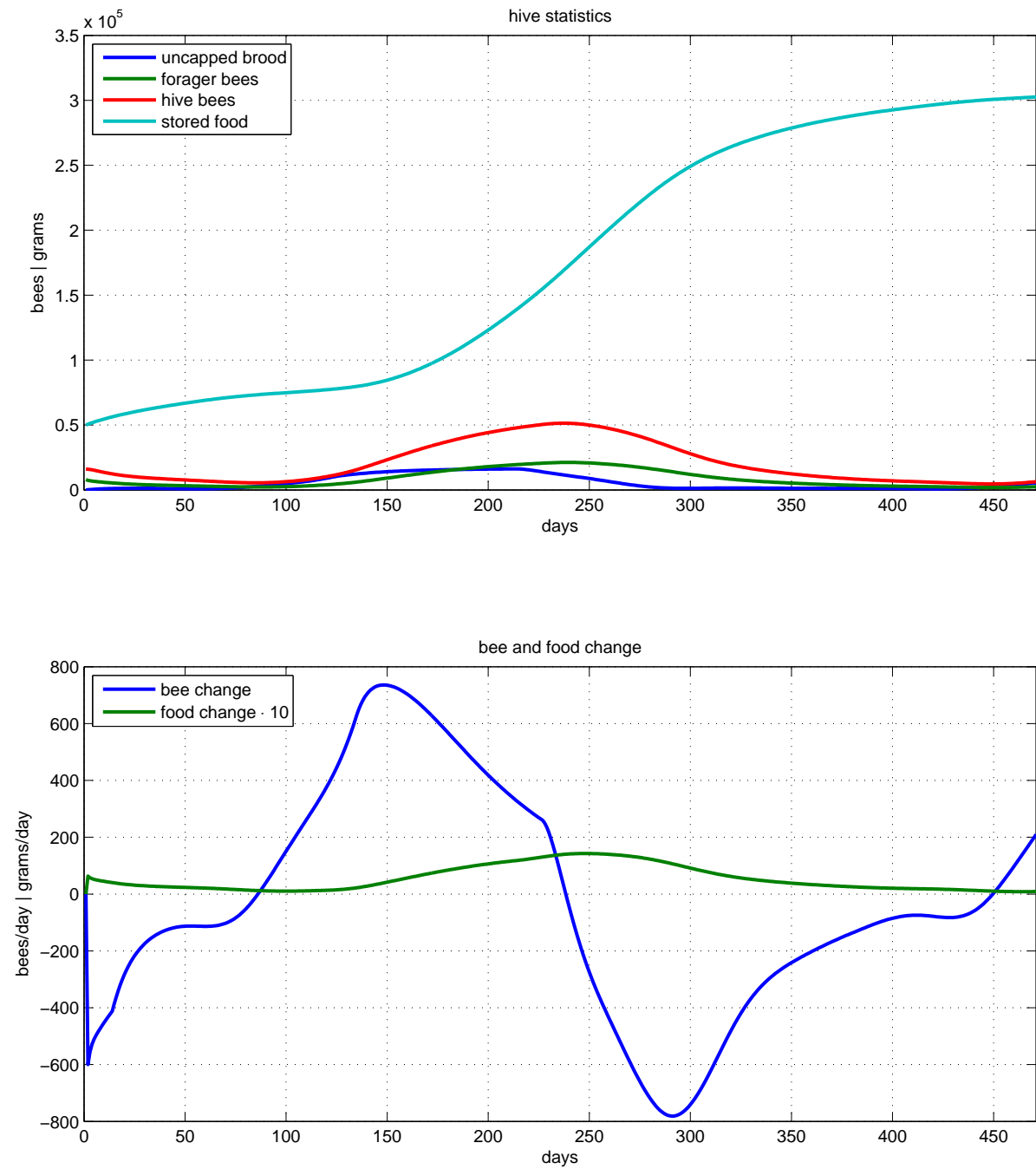
% Start simulation
hive_simulation(proparray);
```



### A.1.2 Constant laying rate, constant food income



### A.1.3 Varying laying rate, constant food income



## A.2 Simulation run with missing flower patches

### A.2.1 Runscript with changes relative to the base properties

```
% This is a runscript for automatized simulation on any system

% Simple test cases based on Properties_Base
run('data\Properties_Base.m');

% Load the properties into memory, make copies and modify them on the go

% The testcases:
% 1. all flowers
% 2. no spring flowers
% 3. no summer flowers
% 4. no autumn flowers

Prop1 = Prop;
Prop1.Sys.identifier = 'Properties_Base_R1_1';

Prop2 = Prop;
Prop2.Sim.Flower(1).year_activity = [1:2;0,0];
Prop2.Sys.identifier = 'Properties_Base_R1_2';

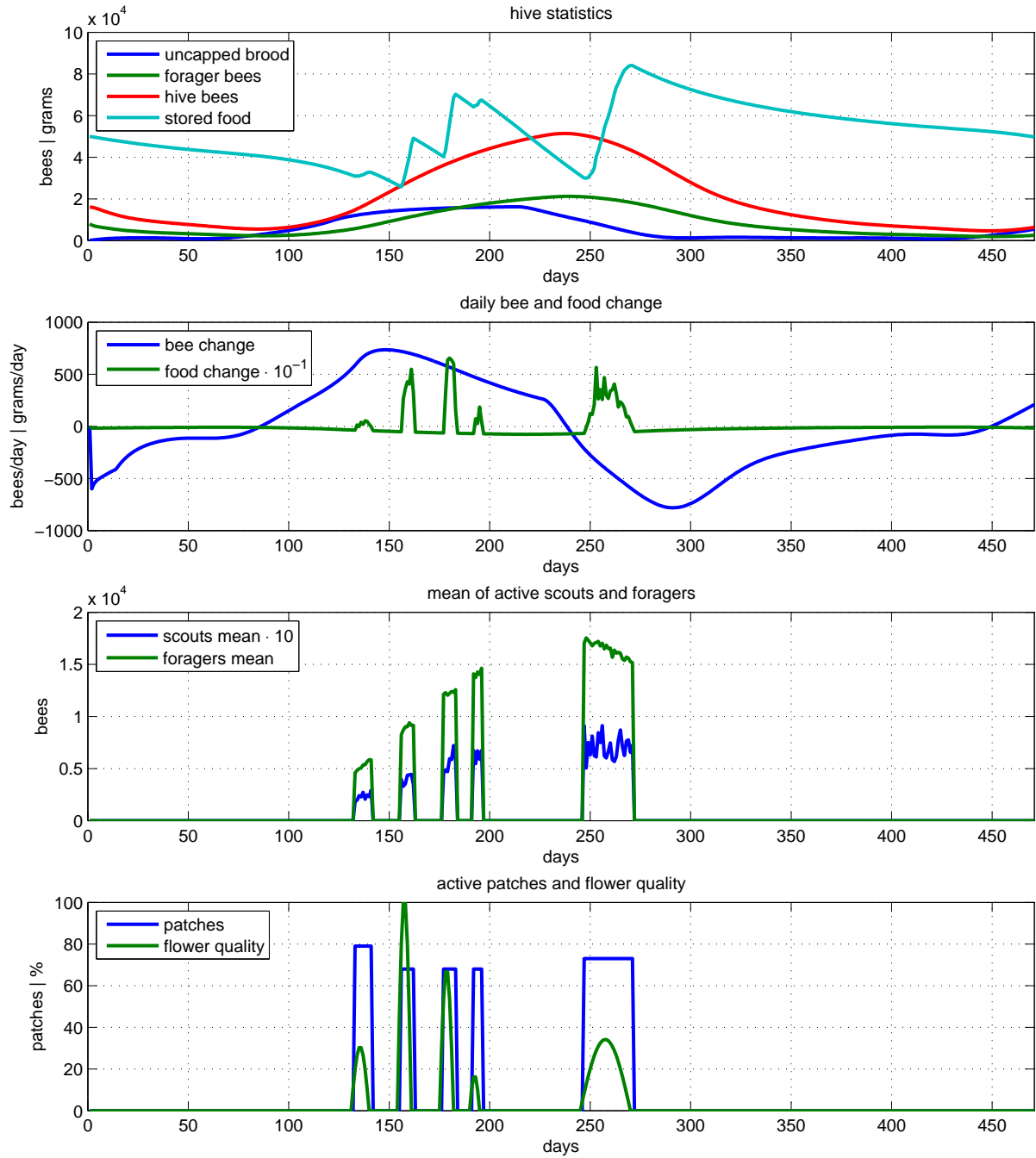
Prop3 = Prop;
Prop3.Sim.Flower(2).year_activity = [1:2;0,0];
Prop3.Sys.identifier = 'Properties_Base_R1_3';

Prop4 = Prop;
Prop4.Sim.Flower(3).year_activity = [1:2;0,0];
Prop4.Sys.identifier = 'Properties_Base_R1_4';

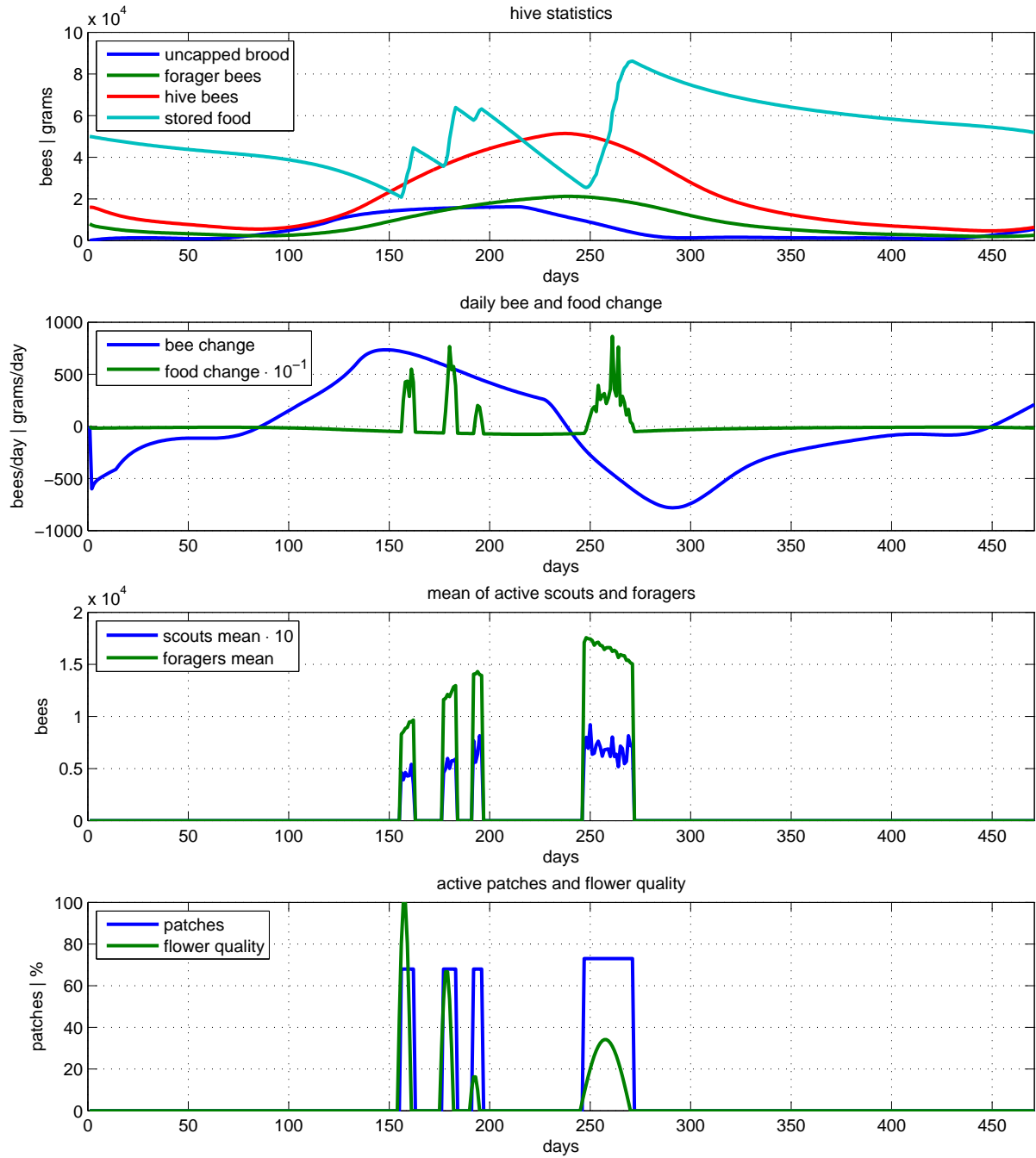
proparray=[Prop1,Prop2,Prop3,Prop4];

% Start simulation
hive_simulation(proparray);
```

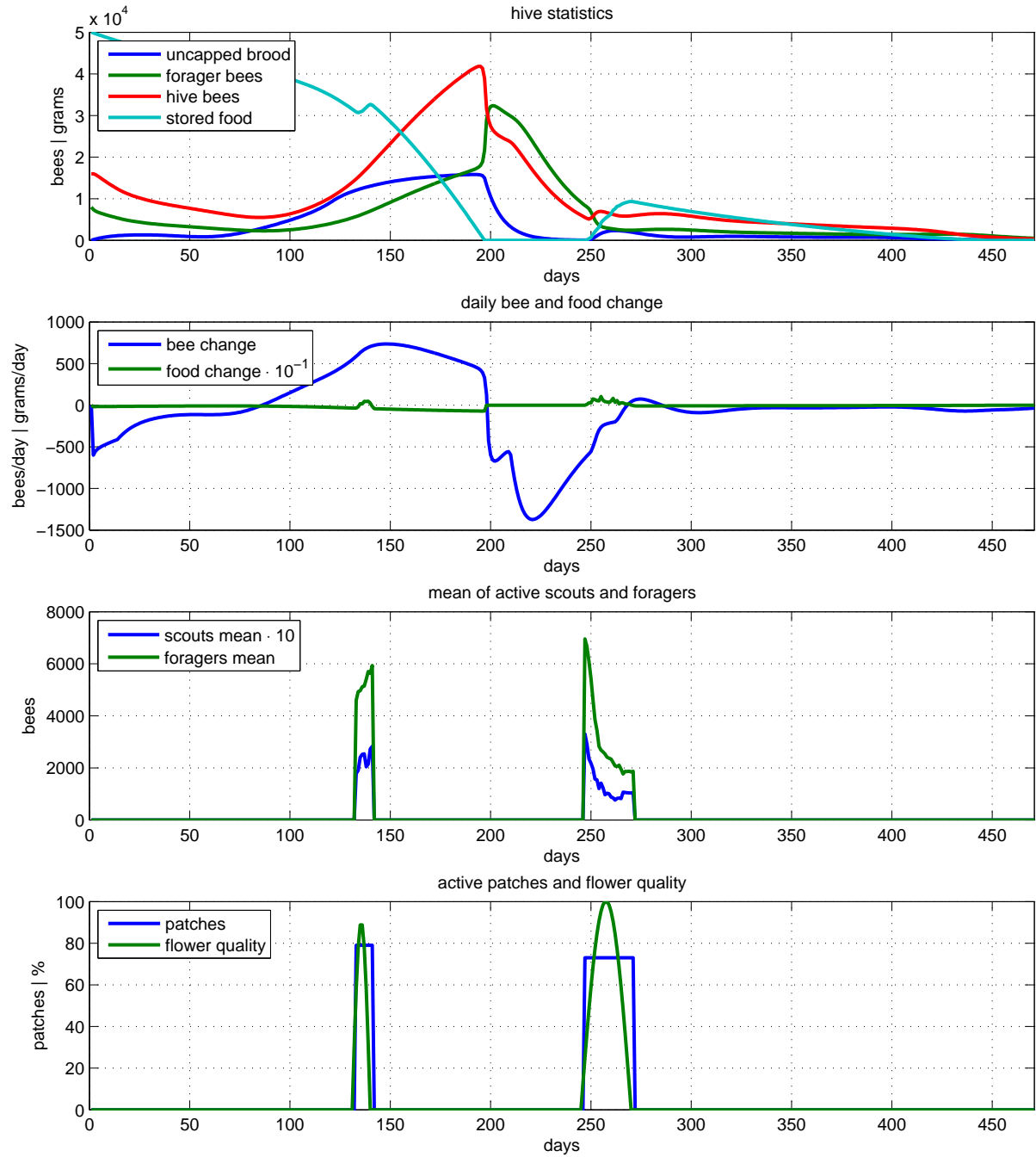
## A.2.2 All flower patches



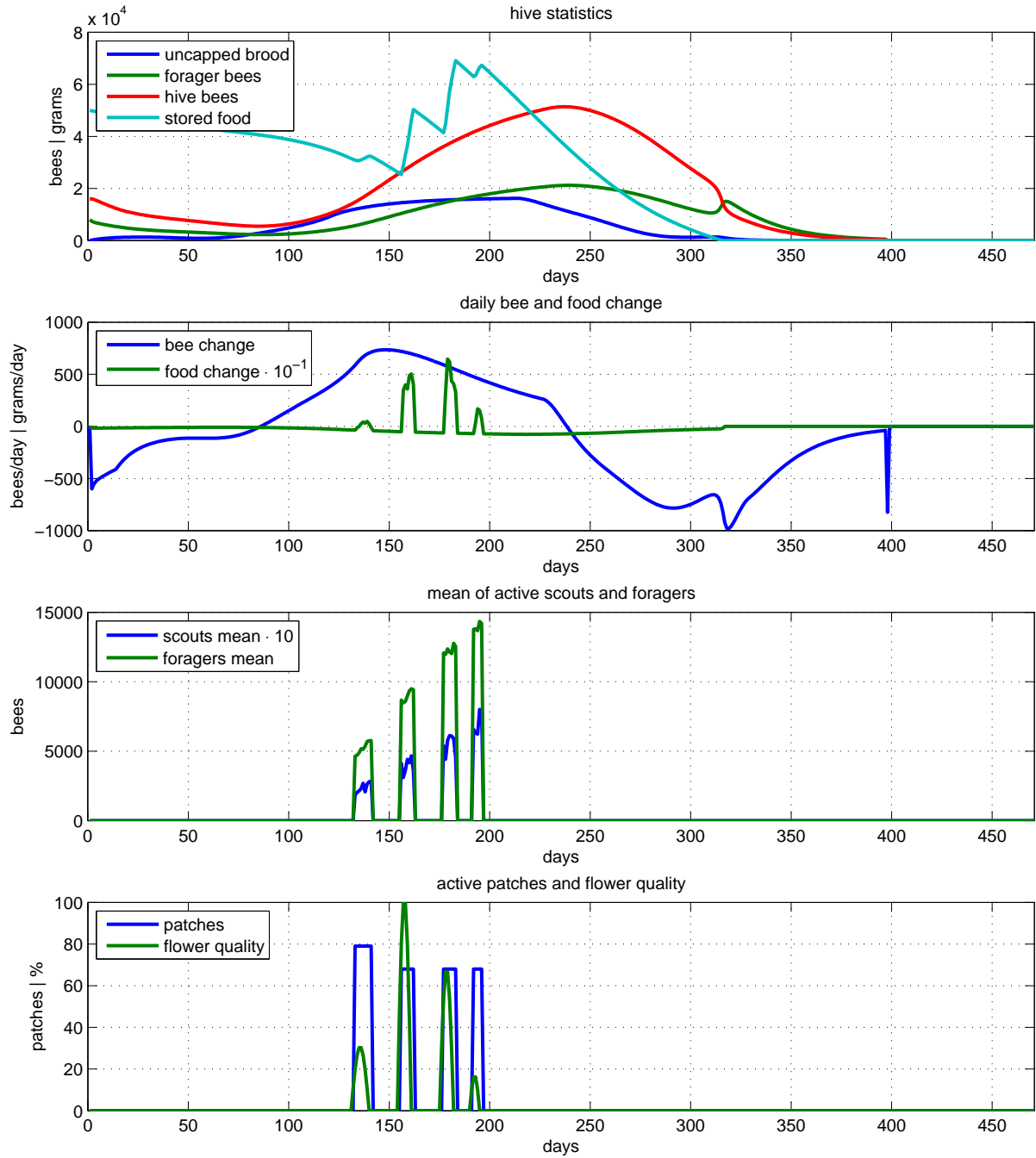
### A.2.3 Missing spring flowers



### A.2.4 Missing summer flowers



### A.2.5 Missing autumn flowers



## A.3 Simulation run with varying autumn flowers

### A.3.1 Runscript with changes relative to the base properties

```
% This is a runscript for automatized simulation on any system

% Simple test cases based on Properties_Base
run('data\Properties_Base.m');

% Load the properties into memory, make copies and modify them on the go

% The testcases, variable change 1:
% 1. Autumn flower peak = 2
% 2. Autumn flower peak = 1.5
% 3. Autumn flower peak = 1
% 4. Autumn flower peak = 0.5

% The testcases, variable change 2:
% 1. Autumn flowers shifted by 4 days
% 2. Autumn flowers shifted by 8 days
% 3. Autumn flowers shifted by 12 days
% 4. Autumn flowers shifted by 16 days
% 5. Autumn flowers shifted by 20 days

% Empty proparray at first
proparray = [];

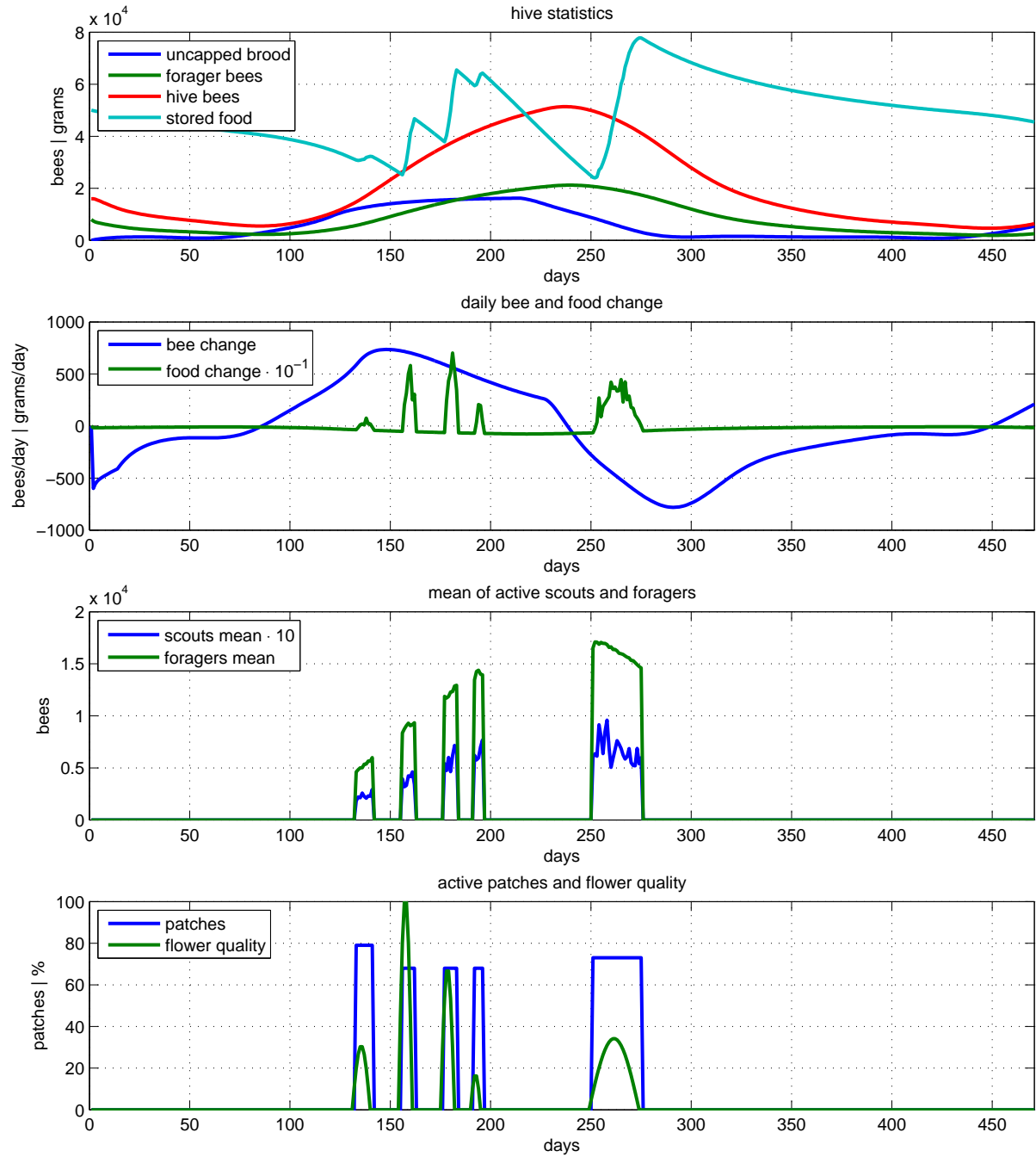
% 4 possible peaks to test
peaks = [2,1.5,1,0.5];

for j=1:5
    for i=1:4
        identifier = strcat('Properties_Base_R2_',num2str(i),'_',num2str(j));
        tprop = Prop;
        tprop.Sys.identifier = identifier;
        tprop.Sim.Flower(3).year_activity(1,:) = tprop.Sim.Flower(3)
            .year_activity(1,:) + j * 4;
        tprop.Sim.Flower(3).peak = peaks(i);
        proparray = [proparray, tprop];
    end
end

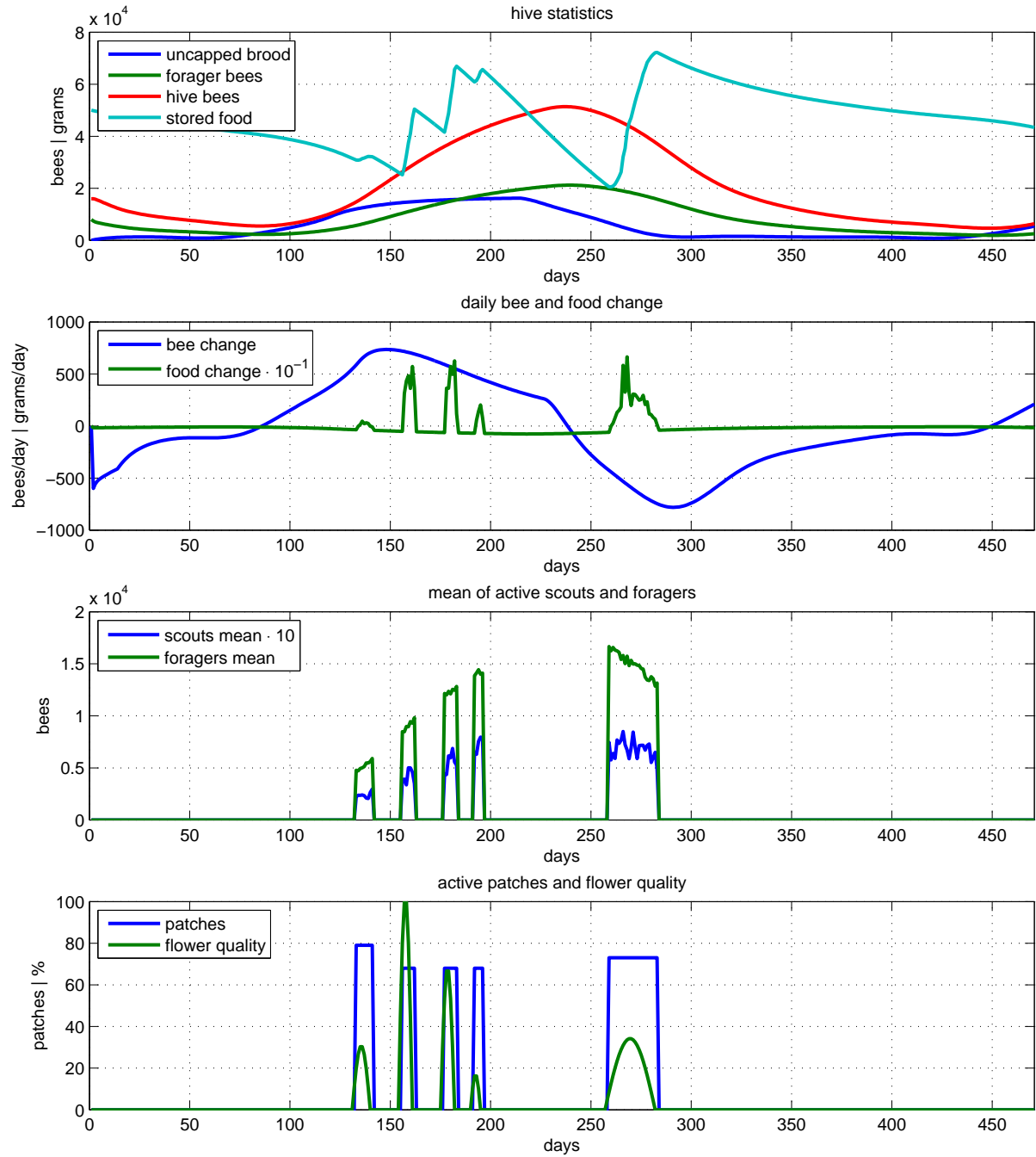
% Start simulation
hive_simulation(proparray);
```



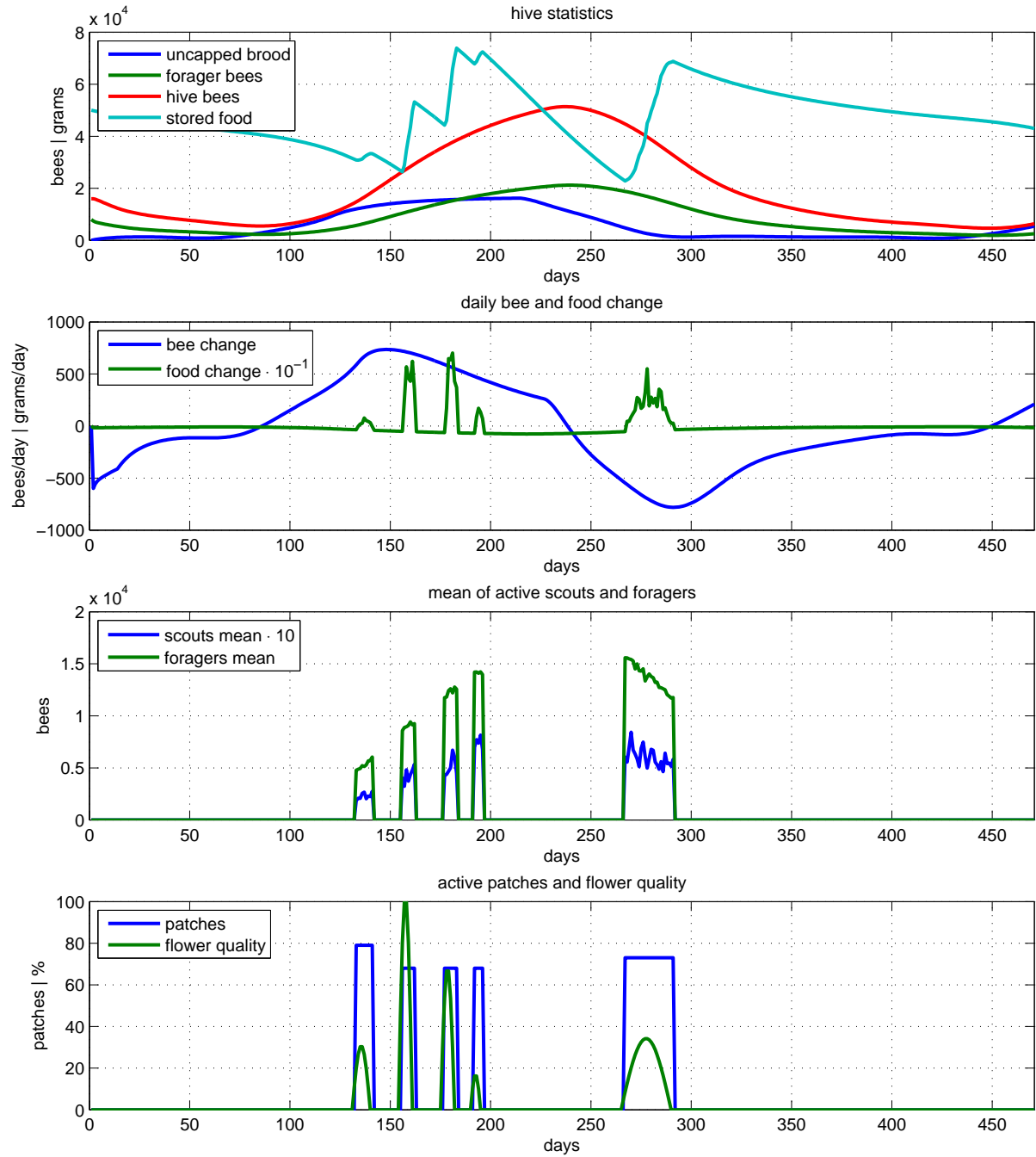
### A.3.2 Peak $M = 2$ , delayed by 4 days



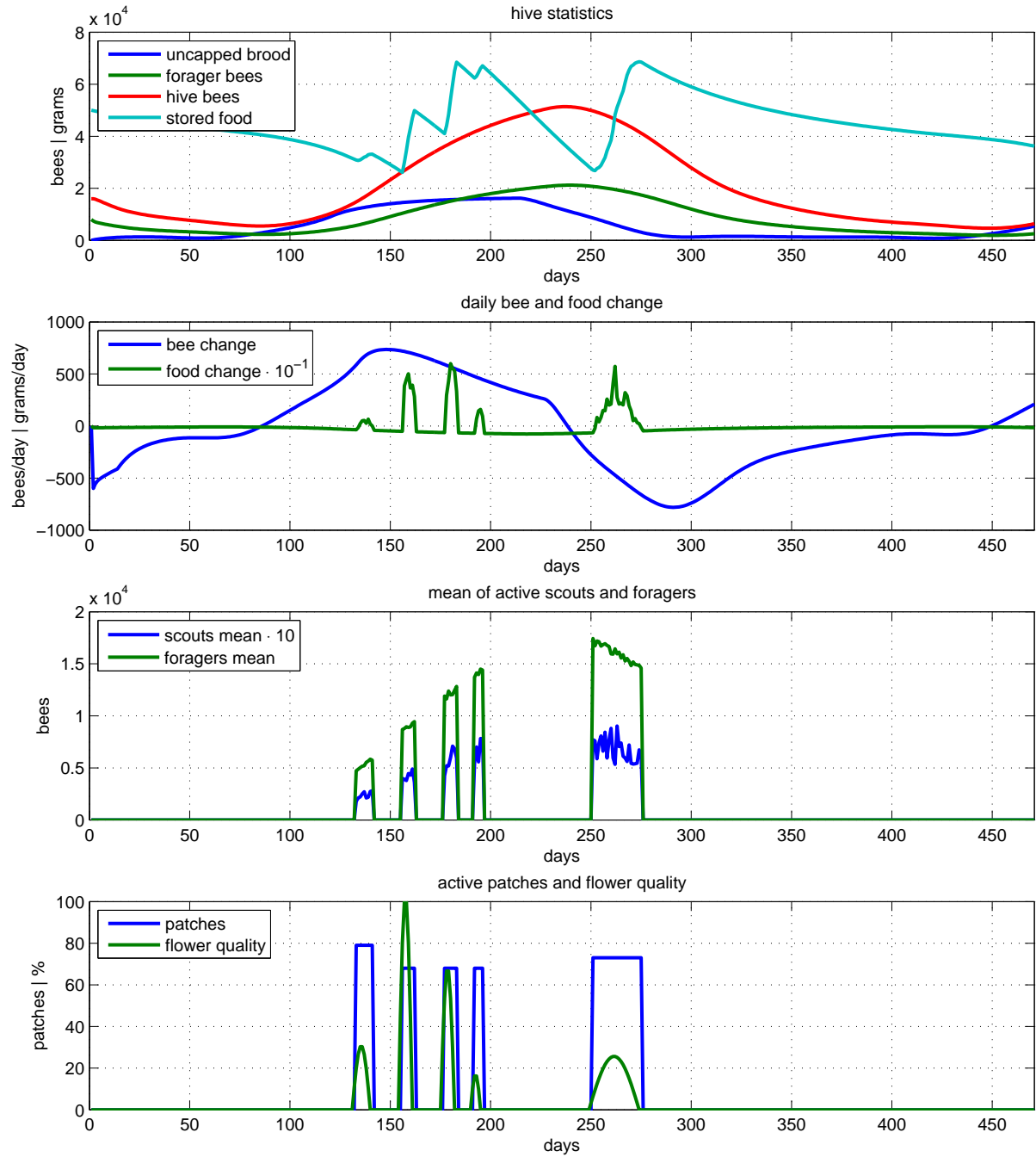
### A.3.3 Peak M = 2, delayed by 12 days



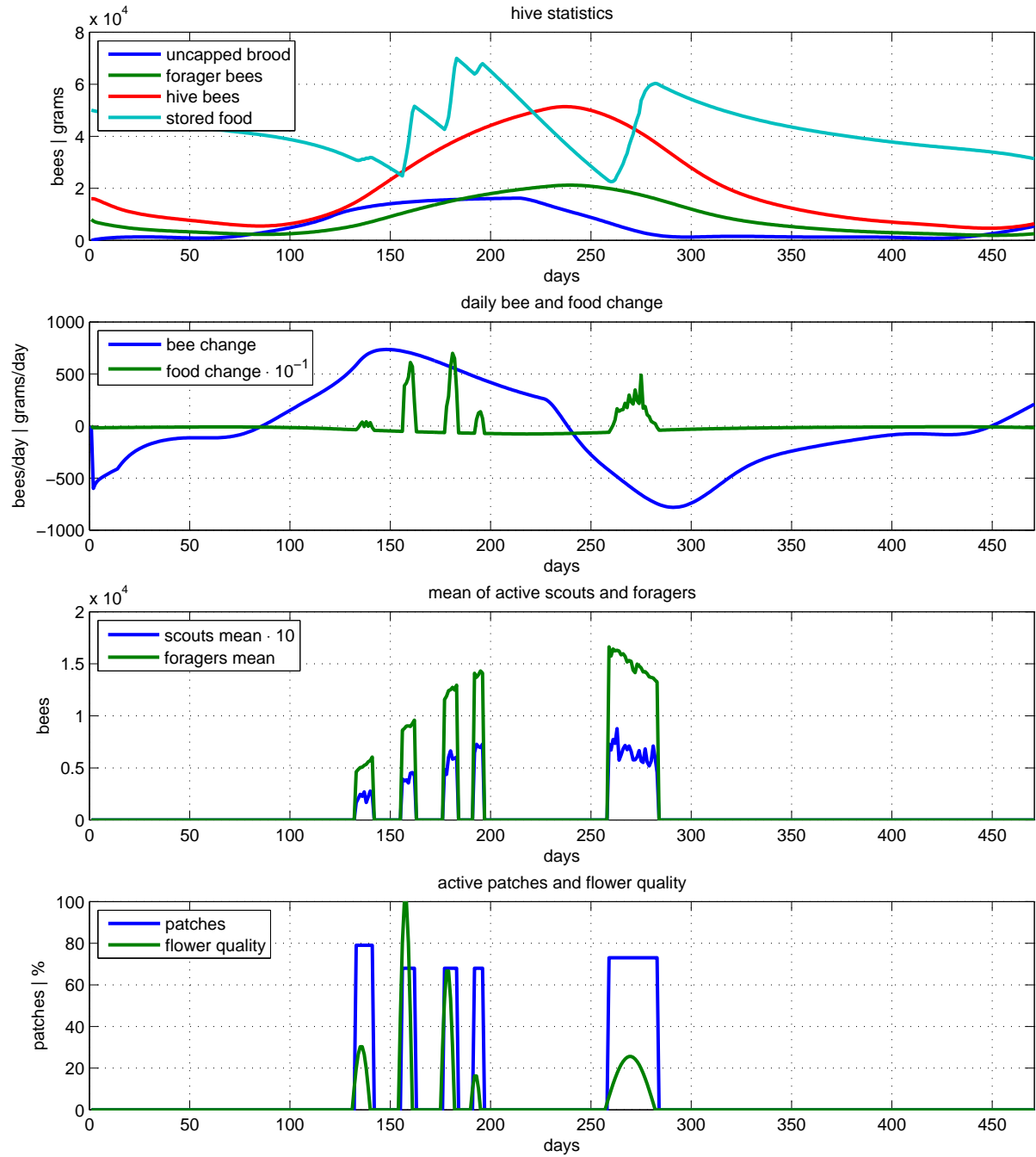
### A.3.4 Peak $M = 2$ , delayed by 20 days



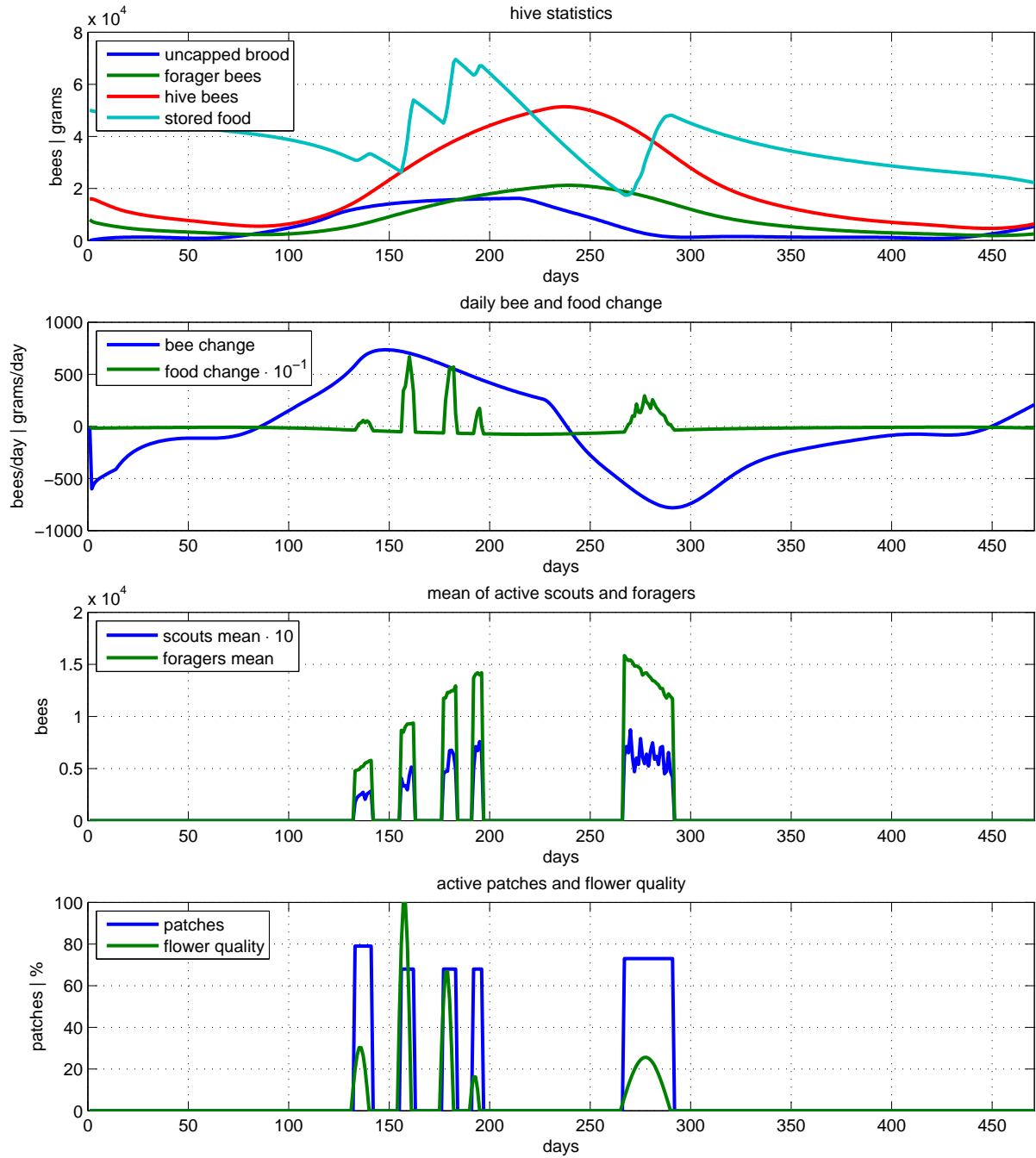
### A.3.5 Peak $M = 1.5$ , delayed by 4 days



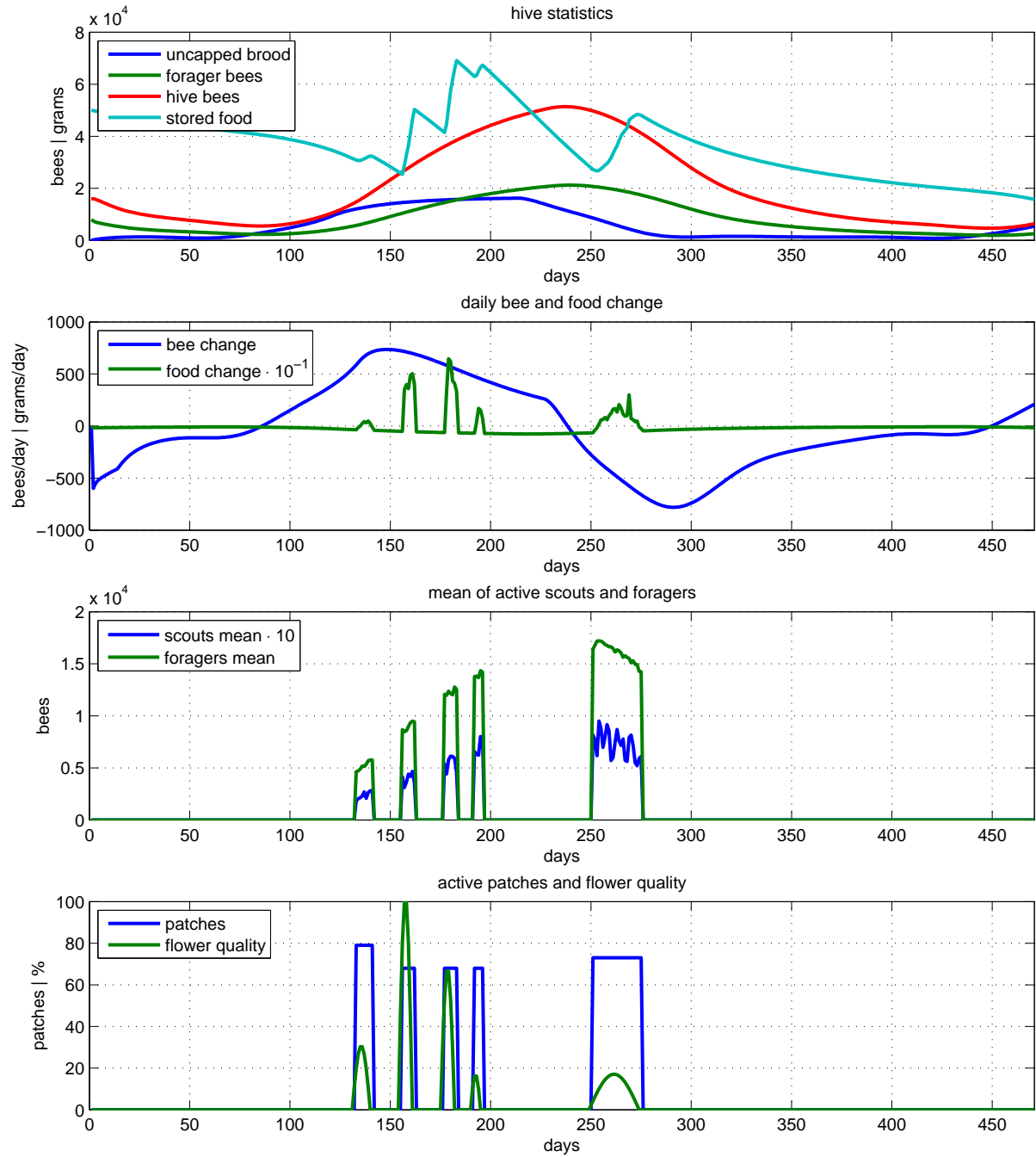
### A.3.6 Peak M = 1.5, delayed by 12 days



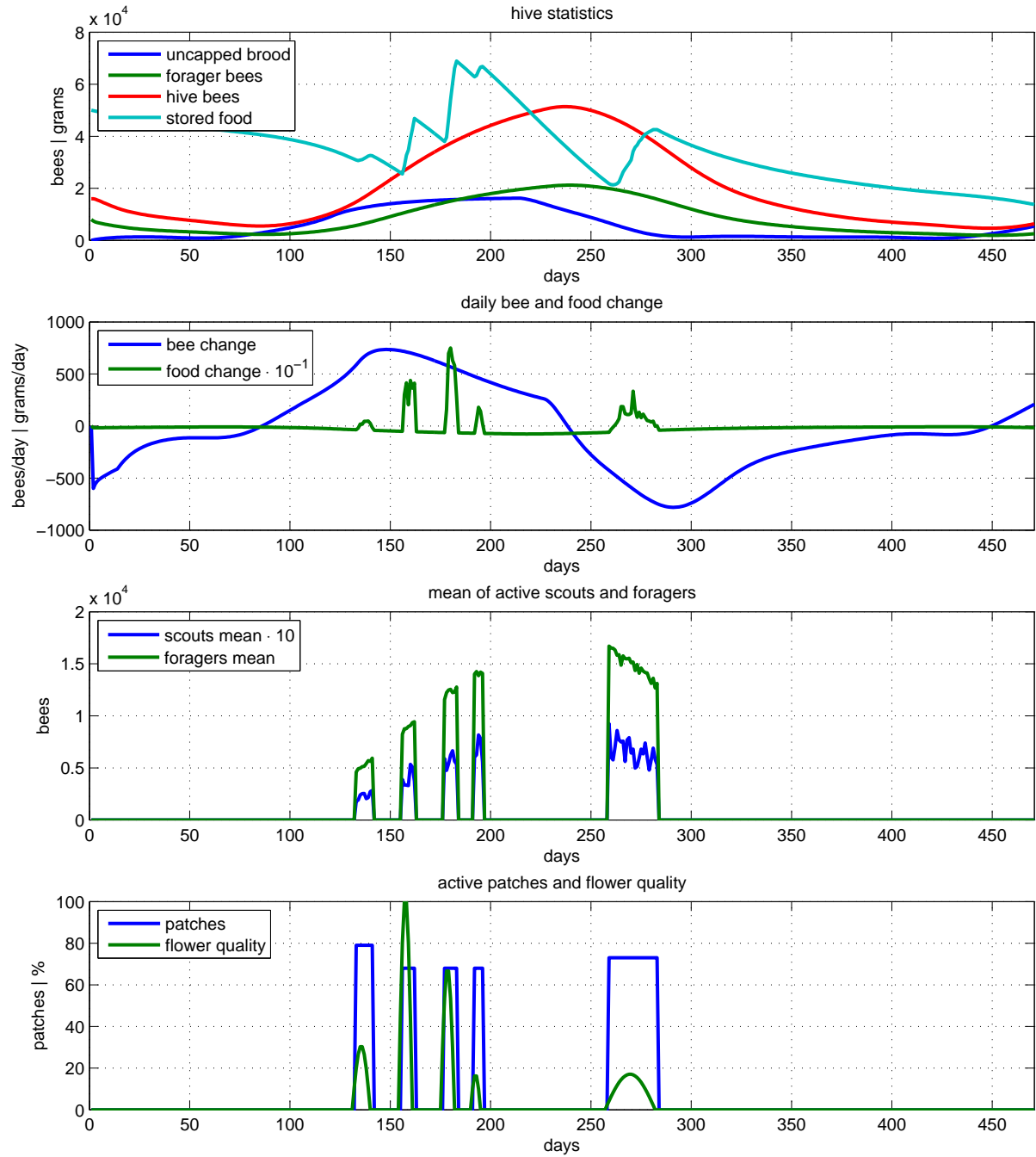
### A.3.7 Peak $M = 1.5$ , delayed by 20 days



### A.3.8 Peak $M = 1$ , delayed by 4 days

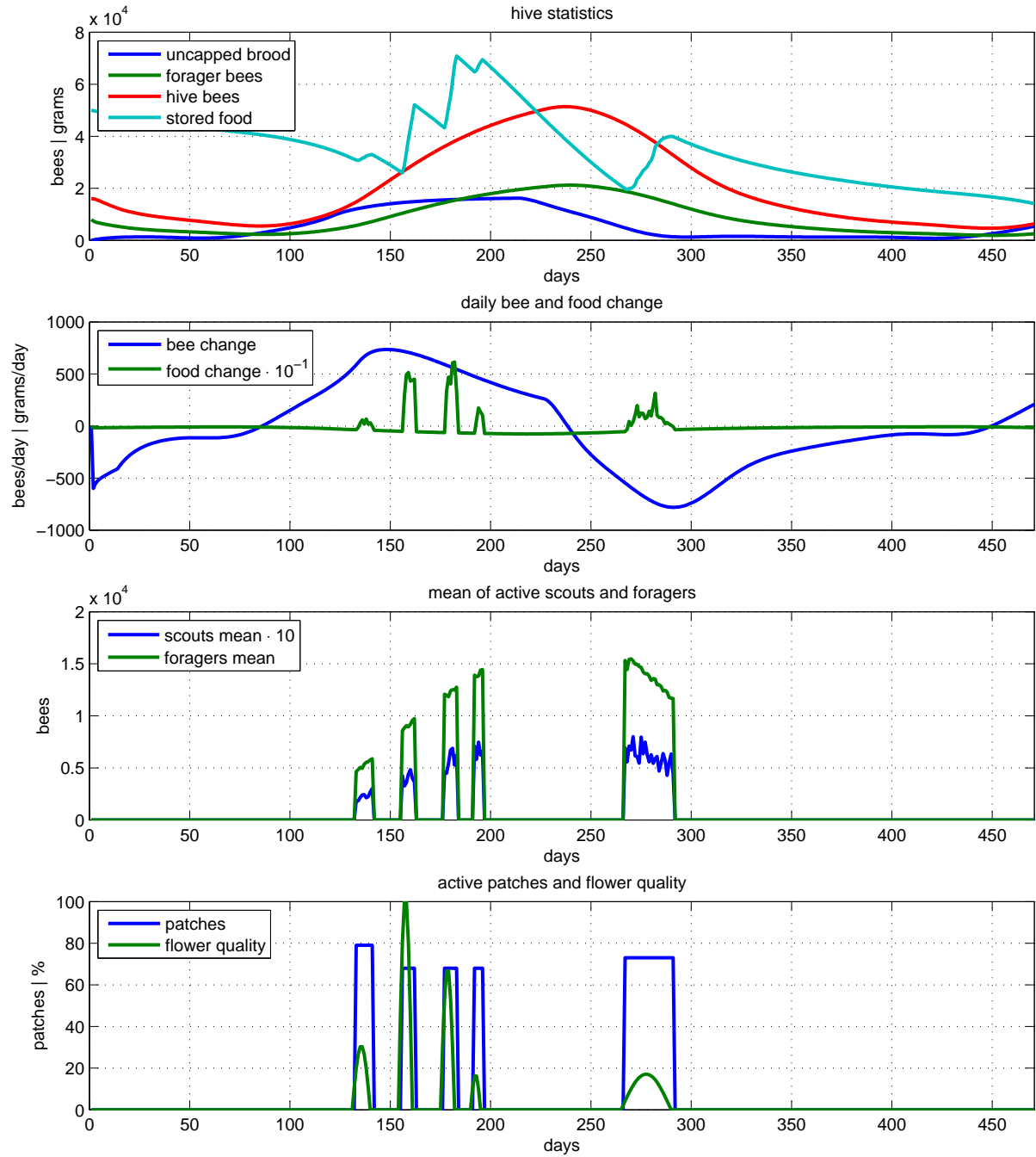


### A.3.9 Peak $M = 1$ , delayed by 12 days

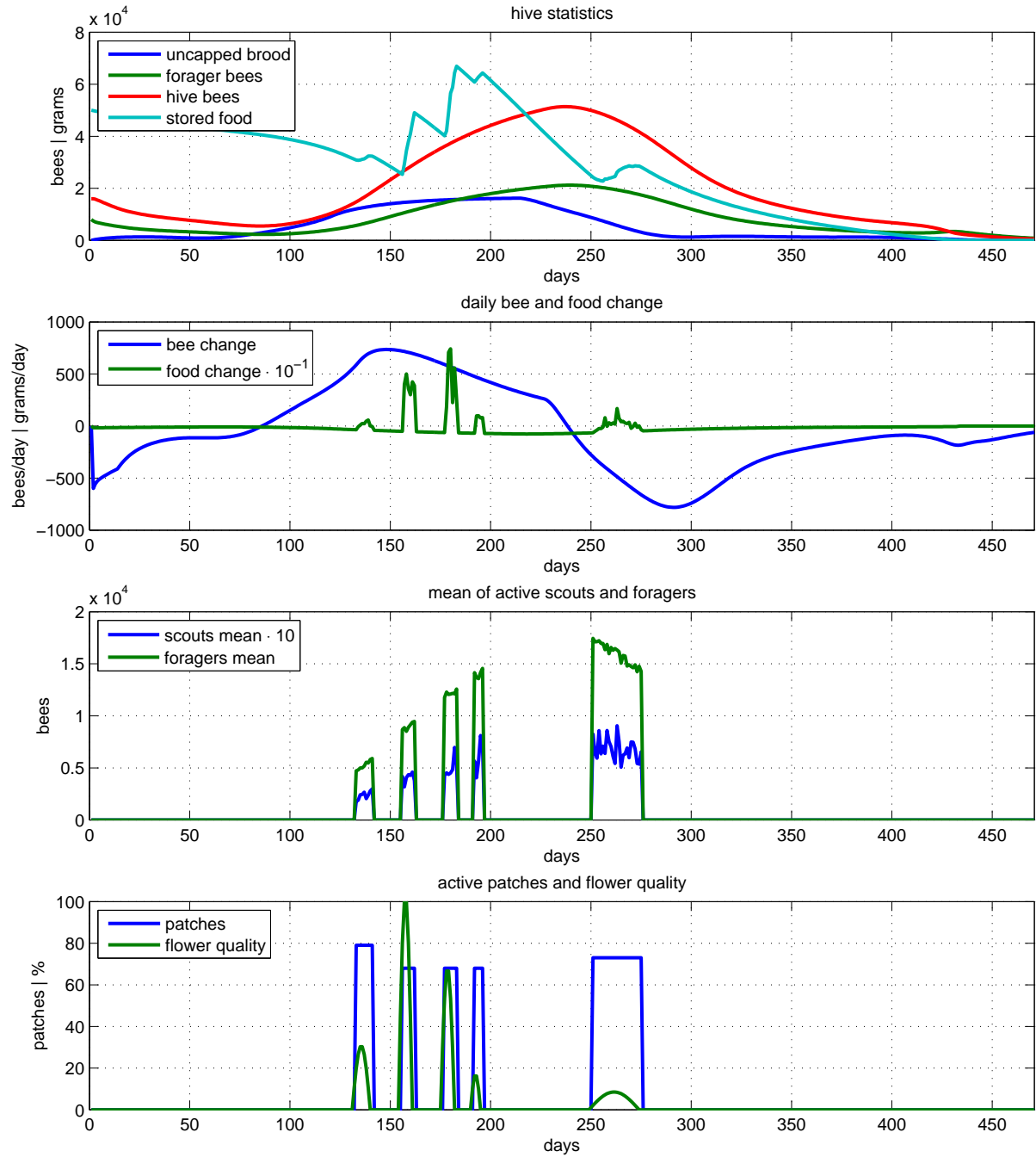




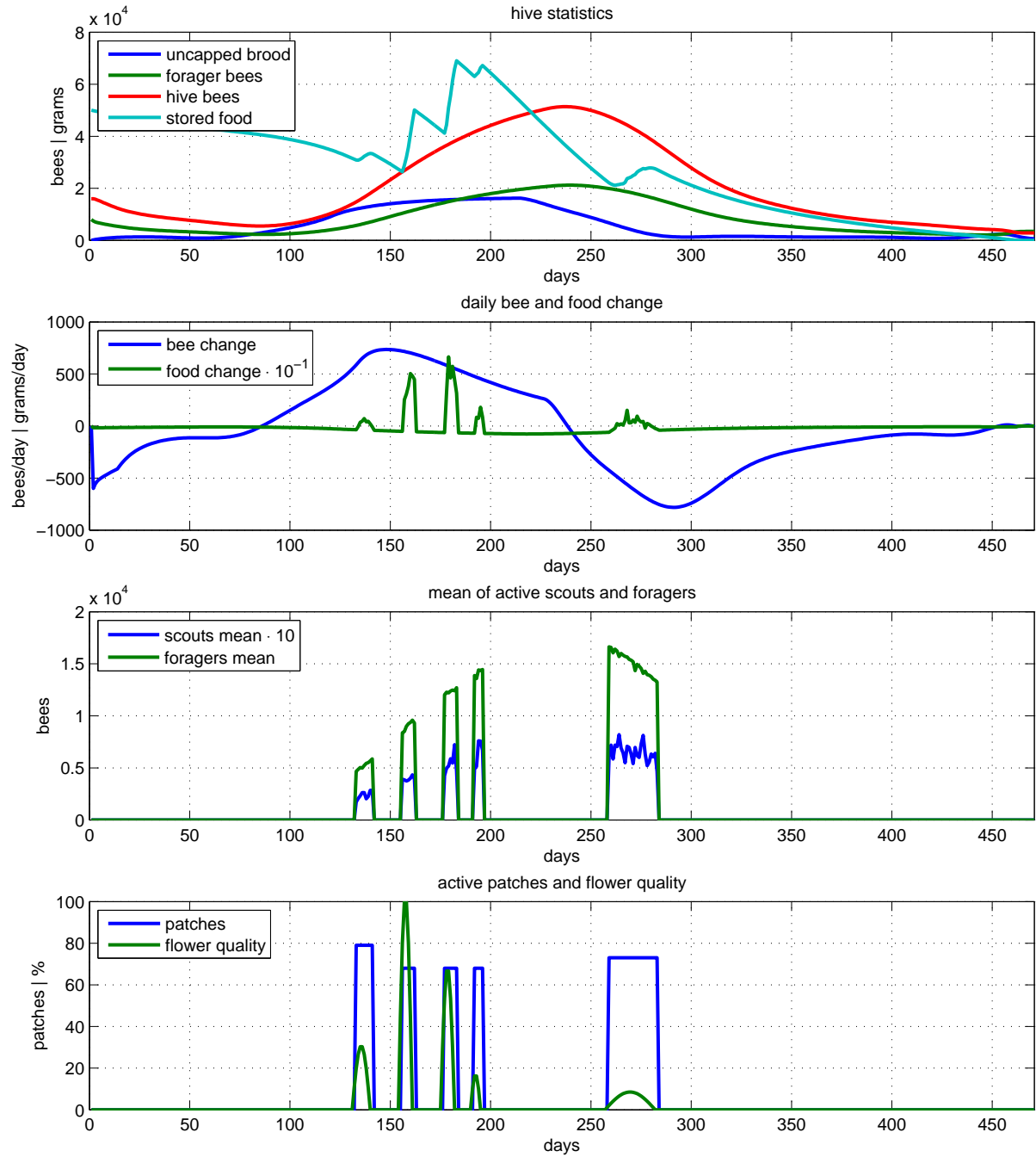
### A.3.10 Peak M = 1, delayed by 20 days



### A.3.11 Peak $M = 0.5$ , delayed by 4 days



### A.3.12 Peak $M = 0.5$ , delayed by 12 days



### A.3.13 Peak $M = 0.5$ , delayed by 20 days

