BEEWARE!
A honeybee colony model

- Investigating the mechanisms of early spring colony collapse -

The 2022 System Dynamics Conference
Frankfurt, Germany

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1. Abstract

Pollinators play a crucial role in most terrestrial ecosystems and provide an important service in maintaining agricultural productivity. About 35% of global crop production is dependent on animal pollination, of which the majority is provided by insects, especially bee species. This is however a fragile system as different environmental factors can dramatically affect the social honeybee dynamics.

In Norway, the Hardanger Fjord is among the countries main fruit production areas and dependent on migrating beekeepers to provide beehives, achieve sufficient pollination rates and maintain yields. However, honeybee colonies are regularly observed to be collapsing in early spring or stagnate in population buildup. This behavior is problematic for all three stakeholders involved: the bees, the beekeepers and the fruit farmers. Weak populations have a low chance of surviving the next winter, a loss of colonies and the potential honey-crop result in economic losses for the beekeeper and fruit producers might gain insufficient pollination rates, potentially reducing yields, crop quality and economic returns.

A honeybee colony model has been developed to explore the basic population dynamics shaping colony development. It uses an aging chain to explore the internal work distribution and its response to external factors. It is implemented in Stella Architect and based on apicultural literature describing the social honeybee behavior and recruitment mechanisms. With the focus of interest being on the interactions of honeybee colony development and fruit production, the simulation covers a 120-day period from the initial post-winter colony development to the respective pollination periods in spring.

The resulting model is able to realistically reproduce, both healthy population development and failure modes such as stagnation and collapse. The performed sensitivity analysis suggests that the overall behavior is strongly dependent on the initial state of the colony. Relevant tipping points have been identified. The colonies survival is furthermore dependent on its ability to build up sufficient energy (honey) supplies, which is influenced by the local food availability, forager bee recruitment and mortality rates. The latter is in turn affected by pathogens and local farming practices.

The model focusses on the fundamental high level social interactions. It fulfills its purpose as a tool for beekeepers and farmers to highlight and visualize the importance of key parameters and shocks on the overall honeybee-colony and pollination performance. It can be further extended beyond its initial purpose by adding further biology driven behavioral dynamics and taking additional endogenous and exogenous factors of interest into account.

2. Problem Identification

Pollinators play a crucial role in most terrestrial ecosystems and provide an important service in maintaining agricultural productivity. About 35% of global crop production is dependent on animal pollinators (Klein, Alexandra-Maria, 2006, p. 1). Insects are the primary pollinators of most wild plants and agricultural crops, of which the majority is pollinated by bees. Their economic value is estimated to be more than 200 billion dollars per year worldwide (Lebuhn et al., 2013). However, the value for natural ecosystems and their respective services is believed to be immensely greater, yet difficult to quantify.

The phenomenon of worldwide declining pollinator populations has gained an increasing awareness in the past (Potts et al., 2010). On top of land change use, pesticides and pollution climate change is putting increasing pressure on pollinator populations. Wild species increasingly fail to provide adequate pollination services for agricultural production. Domesticated honeybees can be effectively bread and relocated for this purpose. The European Honeybee *Apis Mellifera* is therefore kept by beekeepers for pollination services and honey production around the globe (Lindström et al., 2016). Yet the number of managed honeybee colonies has suffered from a significant reduction over the past decade in many parts of the world (Hristov et al., 2020).

In Norway, the Hardanger Fjord is among the countries main fruit production areas and dependent on migrating beekeepers to achieve sufficient pollination rates and maintain yields. About 250 beehives are therefore moved from the greater Bergen region to the Hardanger Fjord in early spring each year. During the long and cold Nordic winters with unfavorable climate conditions, the bees are bound to the hive, do not multiply and need to survive on limited honey reserves. Once spring starts with rising temperatures and increasing daylight, the colony increases its activity and initiates reproduction. A typical spring population development is shown in Figure 1 (l).

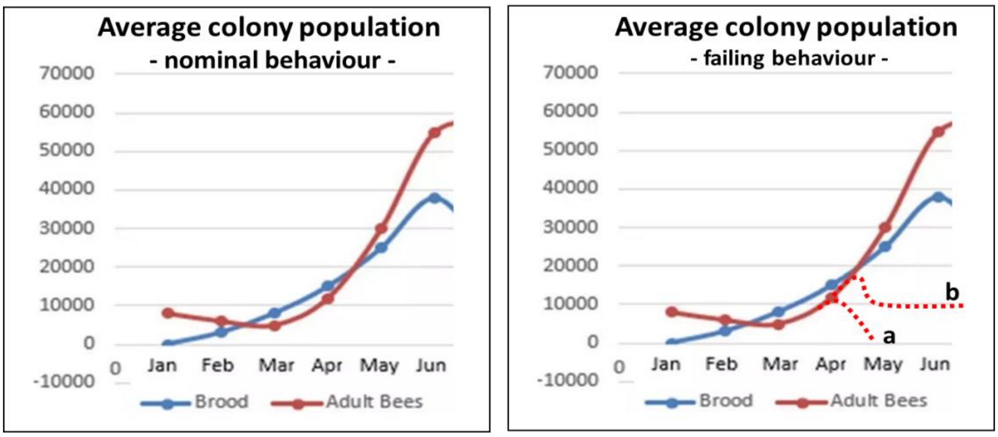


Figure 1: Reference mode: nominal colony development (l) and failing colony development (r)

However, some colonies are regularly observed to be collapsing in early spring as shown in Figure 1 (r). The problematic scenarios a) and b) are based on interviews with local beekeepers and represent the qualitative behavior of typical failure modes. The quantitative values might vary from case to case. In scenario a) the colony fails to build up in strength and collapses. In this case the beekeeper finds a deserted hive under inspection and on some occasions a number of dead bees in the immediate surrounding of the hive, with either low or depleted honey stocks present. In scenario b) the colony slowly builds up and stalls. The development stagnates at a low population level despite sufficient food reserves being present. The timing of these events seems surprising as the colonies managed to survive a long winter under harsh conditions, just to collapse when the tides turn, and favorable spring conditions occur.

This behavior is problematic for all 3 stakeholders involved: the bees, the beekeepers, and the fruit farmers. Weak populations have a low chance of surviving the next winter, a loss of colonies and the potential honey-crop result in economic losses for the beekeeper (on top of the ethical burden of losing the animals one was responsible for) and apple farmers might gain insufficient pollination, potentially resulting in reduced yield and crop quality.

3. Hypothesis

To understand and model the underlying colony population dynamics it is crucial to understand the basics of honeybee biology and behavior.

Each colony has one single reproductive member, the queen-bee. She can lay up to 3000 eggs per day (Wei et al., 2019), which hatch after 3 days and enter the brood stage. The brood (larvae and pupae) needs to be actively fed and warmed by adult worker bees. This process is referred to as *rearing* in the remainder of this paper. The brood develops into female worker bees (ca. 95%) and male drones (ca. 5%) which takes 21 (worker bee) or 24 (drone) days.

The drone's sole purpose is to mate with virgin queens from other colonies during late spring and summer. They generally do not contribute to the colony's internal dynamics other than that.
All worker bees are sterile and morphologically identical, but specialize on different tasks depending on age, colony composition and resource situation (Seeley, 1995). Worker bees can be sub-divided in two main distinct and discrete casts: hive-bees and forager bees.

Newborn honeybees spend the first part of their lives as hive-bees. Members of this cast do not leave the hive and take on different behavior roles within the colony. The majority of a bee's hive-bee career is assigned to brood rearing, followed by subsequent roles that include building honeycomb, cleaning, guarding and honey processing (Seeley, 1995).

Hive-bees finally transition to forager bees for the last part of their lives. Foragers leave the hive to collect water and floral resources. This includes pollen (protein) and nectar (energy), which is either consumed upon arrival in the colony or processed to honey for storage.

A colonies fate is highly determined by the dynamic interactions between the different casts and their ability to actively manage growth (brood rearing) and energy resources (food) in accordance with the current state and composition of the overall colony.

The dynamic hypothesis for the reference mode (Figure 1) is mainly determined by bee biology and presented in the form of a simplified causal loop diagram (CLD) in Figure 2.

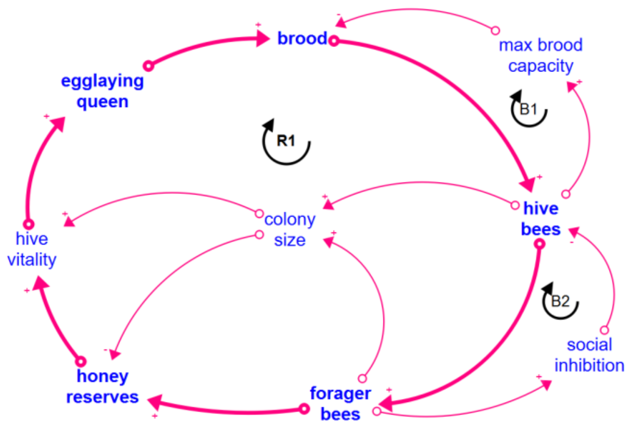


Figure 2: Causal loop diagram for the dynamic hypothesis of population development

During early spring the queen resumes egg-laying at a low rate after having been inactive during the winter months. An increase in eggs, which hatch after 3 days (Collins, 2004, p. 1), leads to an increase of brood present in the colony. For this model different stages of brood (larva, pupae, capped brood) are summarized as brood. After 21 days (Wu et al., 2011, p. 6) the brood emerges and new born bees join the cast of hive-bees. An increase in brood therefore subsequently leads to an increase of hive-bees present in the colony. After a certain period, depending on the condition of the colony, hive-bees transition to forager bees. The larger the hive-bee cast, the more hive-bees will ultimately get promoted and the number of forager-bees increases. An increasing number of foragers leads to an increasing amount of total forager flights. The resulting honey inflow contributes positively to the stock of honey reserves. At the same time honey consumption increases due to an increasing colony size with the brood rearing process being especially energy demanding (Khoury, 2013, p. 3).

Both, an increasing colony size (Khoury et al., 2011, p. 2) and honey inflow (Horn et al., 2016, p. 1) ultimately encourage the queen to gradually increase her egg-laying rate to her maximum capacity of up to 3000 eggs/day (Winston, 1991).

For this model I introduced the term hive vitality**,** which takes both growth driving factors (honey inflow & colony size) into account. The term is defined in a manner that it turns to zero when the colony size turns to zero (a hive without bees has zero vitality). However, it remains positive when bees are present, but the honey inflow turns to zero. This describes the observed behaviour of queens continuing egg-laying during bad weather periods (no flights -> no foraging) and draughts (no nectar flow).

In early spring an increasing hive vitality leads to an increasing egg-laying rate, which closes the main reinforcing loop **R1** in the CLD (Figure 1).

The amount of brood that can be raised simultaneously is limited by the amount of hive-bees already present to rear to brood (Torres et al., 2015, p. 8) as pictured in **B1** of the CLD. Brood that exceeds the max capacity will die due to a lack of care and heating.

The process described in **B2** is called social inhibition. The age at which a hive-bee transitions to a forager bee is determined by social feedback mechanisms within the colony. In a healthy well-balanced colony the group of foragers typically makes up about 1/3 of the overall adult bee population (DeGrandi-Hoffman et al., 1989, p. 145) and the age at which a hive bee transitions to a forager is about 21 days (Fukuda & Sakagami, 1968, p. 33). The transition age is governed by a pheromone, which is produced by the forager bees. An abundance of foragers in relation to the overall population increases the pheromone concentration, which slows down forager-bee recruitment. If there is a shortfall of foragers in the colony, the resulting low pheromone concentration accelerates forager bee recruitment. The minimum age at which a hive-bee can start foraging is 4 days according to (Fahrbach & Robinson, 1996, p. 1). For my model I assume that the pheromone concentration is directly proportional to the number of foragers in the hive and define a linear relation between the ratio of foragers in the colony and the hive-bee transition age. The slope of the relation (called *transition factor* in the model) is chosen to fit the empirical data-points reported in literature of 4 days / 0% foragers and 21 days / 33% foragers. Hence the hive-bee transition age decreases when foragers make up less than 33% of the colony and increases when the foragers exceed 33%. The negative feedback loop **B2** maintains a relatively constant fraction of foragers under steady state conditions.

The CLD in Figure 2 describes the dynamics of bee-production. On the other hand, the colony growth is balanced by the combined deathrates off all honeybee development stages.

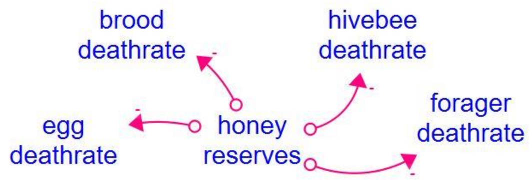


Figure 3: Sufficient honey reserves decrease death-rates to minimum rates

Hive-bees exclusively work under protected conditions within a well-guarded colony. Their baseline mortality rates are relatively low (ca. 0,7%) (Russell et al., 2013, p. 167). The literature reports standard daily mortality rates for eggs and brood of 5,8 % and 9,8% (Fukuda & Sakagami, 1968, p. 34). Forager bees are exposed to predators, pollution, harsh weather conditions, pathogens and face the risk of getting lost. Their death-rate is reported to be up to 15% per day (Dukas, 2008, p. 253).

However, the mortality rates depend on the available energy (honey) reserves. If the honey stock drops below 2 kg the colony starts to show stress behavior (according to beekeeper observation) and below 1,5 kg first starvation symptoms appear due to local food supply insufficiencies, resulting in increasing death-rates. Brood and eggs die first as they are cannibalized by hive-bees to recover energy. It is assumed that the rate for all stages quickly grows to one as the honey stock approaches zero.

According to a literature review multiple groups have been working on models of honeybee colonies. These numerical models are generally based on differential equation systems and have been implemented at different levels of detail while focussing on different aspects of colony development (DeGrandi-Hoffman et al., 1989; Khoury, 2013; Khoury et al., 2011; Russell et al., 2013, Horn et al., 2016). While these models simulate colony development over multiple years, I am particularly interested in early spring failure at given initial conditions as described in chapter 1. I therefore limit my timeframe to the first 120 days (4 months), with day zero being the first day the queen resumes egg-laying after winter.

4. Analysis

Validation

Before running the model and analysing the simulation results various validation tests have been performed to build confidence in the model structure, the underlying mechanisms and the correct execution of the simulation run.

- ***Integration error test***

Running the model on different integration methods (Euler, RK2, Cycle time, RK4) did not affect the observed simulation results. A variation of the integration step varying from a DT of 1/16 to 1 did neither impact the models output.

- ***Dimensional consistency test***
  All parameters have real life equivalents and have been assigned consistent units. A unit analysis by the modelling software Stella Architect does not indicate dimensional inconsistencies.
- ***Structure confirmation test***
  The structure of the various model sectors and the underlying relationships and interactions are based on the literature and knowledge about real life honeybee biology and behaviour. The fundamentals of which are well researched and documented. The according references are stated within this paper, the model documentation, and the model file. A comprehensive list of the referenced literature is given in the bibliography.
- ***Parameter confirmation test***
  All model parameters correspond to real life parameters and the corresponding values are based on the literature referenced in the report, the model documentation, and the model file. Introduced parameters, such as e.g., the "*hive vitality*"-parameter are based on and linked to real life parameters and explained in this paper.
- ***Direct extreme condition testing***
  All model equations have been tested in a stand-alone setting with extreme values for the input parameters. The equations did not generate unexpected behaviour.
- ***Extreme condition test***
  Extreme conditions have been tested on overall model level by varying the input parameters and initial conditions to extreme values beyond practical relevance. The model behaves in a plausible manner and generates comprehensible results in line with expected real-life behavior. Shocks to critical parameters generate plausible behavior.
- ***Behaviour sensitivity test***
  Sensitivity tests have been performed on critical variables. The identified sensitive parameters are addressed within the analysis in the following subchapter and the Annex.
- ***Behavior reproduction***
  Under the tested conditions the model behaves in a plausible manner and generates comprehensible results in line with expected or possible real-life behavior.

Base-case Scenario

The initial colony conditions (hive strength and honey reserves) are defined by the state of the colony on the day the queen resumes egg-laying after winter dormancy. This is also defined as day 0 within the time horizon of the model simulation.

The initial conditions of the base-case scenario are based on beekeeper experience under local conditions in line with the literature and are set to an initial hive-bee population stock of 5000 hive-bees and 5kg of honey stocks. While the initial hive-strength is mainly defined by the colony's performance in the previous season, the initial honey supply depends on external factors such as the amount of food provided by the beekeeper in fall and the winter consumption, which is sensitive to climate conditions.

The average amount of flights per day within the simulated period is based on the maximum amount of 13,5 reported under perfect weather conditions (Rodney & Purdy, 2020, p. 167) and reduced by 40% to 8 flights/day to account for days with unfavorable flight conditions. This parameter was also subject to a sensitivity analysis (Appendix).

The queen's maximum egg-laying capacity is a genetically defined trait influenced by the queens age and, according to the literature (Wei et al., 2019, p. 1), is set to 3000 eggs per day for the base-case-scenario.

Under these conditions the simulation run generates a dynamic behavior (Figure 4) of the adult colony population that qualitatively resembles the reference mode of a healthy colony development in Figure 1. The overall development is characterized by an initial linear decline (A) followed by a subsequent growth- (B) and saturation- phase (C), which peaks at around 25.000 bees. The maximum colony size is mainly determined by the queen's maximum egg- laying capacity and the forager bee death-rate. For which I have chosen average values based on the literature (model documentation in APPENDIX). Under optimal conditions (high egg production, low forager deathrate) colonies can build up to around 45000 individuals.

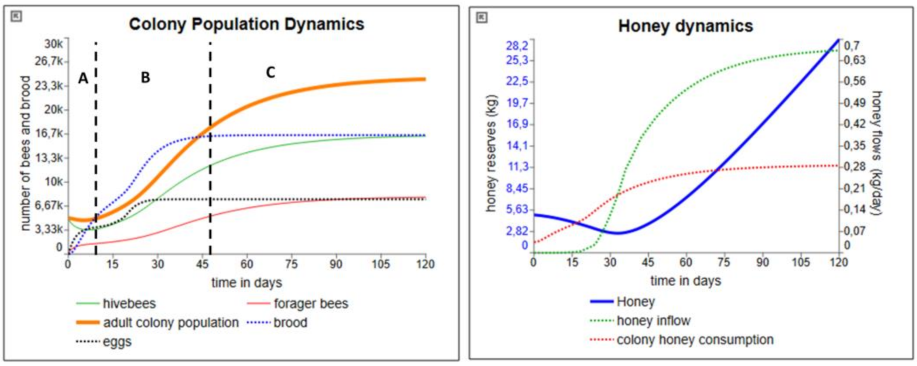


Figure 4: Population (l) and honey(r) dynamics under baseline initial conditions.

The initial decline in phase A is driven by an early transition of hive-bees from the hive-bee stock to the forager stock. Foragers are subject to a significantly higher deathrate than the initial hive-bee population (Figure 5.) The transition-rate is dependent on the fraction of foragers already present in the hive, which is zero (by definition) on day zero (bees do not forage in winter). Hive-bees therefore transition at the minimum possible age (Figure 5) and the forager stock quickly increases, which in return increases the forager recruitment age and slows down the transition as described in the social inhibition loop B2 in the CLD presented in Figure 2.

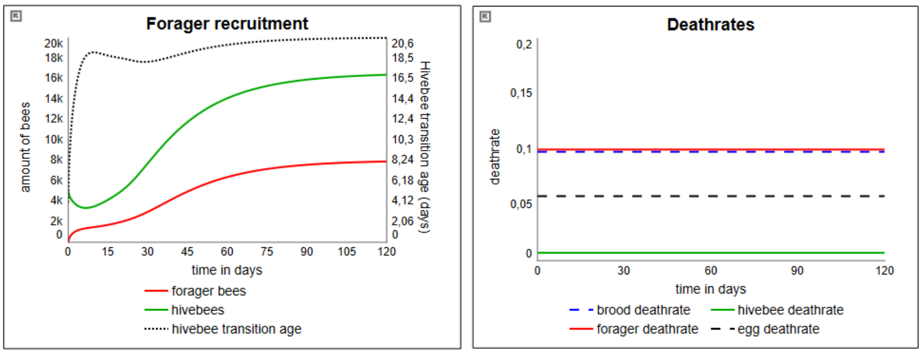


Figure 5: forager bee recruitment (l) and the respective death-rates (r)

While the colony declines during phase A the queen initiates egg-laying. The rate of which is driven by the hive vitality as shown in Figure 6.

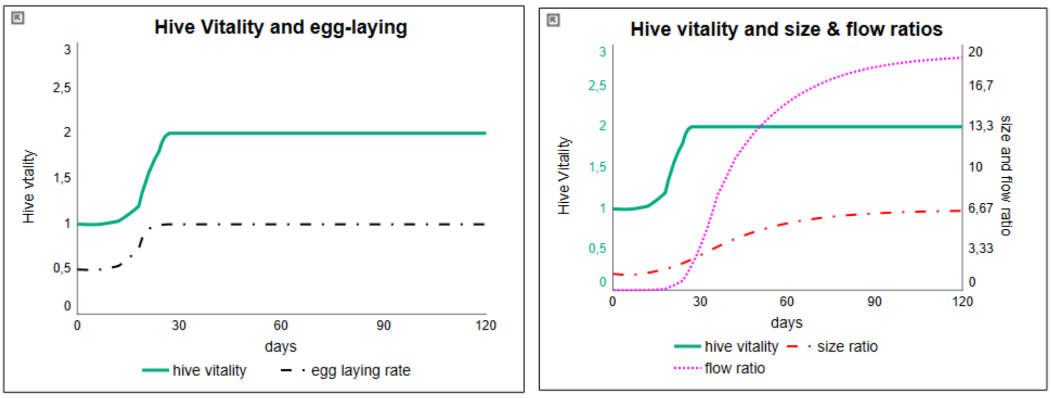


Figure 6: hive-vitality dependent on colony size and nectar flow ratios (l,) corresponding egg-laying rate (r)

The hive vitality depends on colony size in relation to the minimal size at which the queen can maintain egg-laying, and the inflow of honey in relation to honey consumption. Both, an increasing colony size and net honeyflow increase hive-vitality. The increase of which is governed by the underlying table function in accordance with literature and observation.

While the initial flow ratio is zero (little foragers and food availability), the initial hive-bee stock of 5000 individuals results in a size ratio of 1,3 and drives hive vitality to an initial value of one, causing the queen to start laying eggs at 50% of her maximum capacity. Delayed by the average development time from egg to hive-bee, the colony consequently produces new bees at a higher rate than the combined mortality rates of all adult bees and enters the growth-phase, labelled B in Figure 4.

A growing colony and an increasing honey inflow, caused by an increasing forager population in combination with improving food availability in early spring (crocus, hazel, and willow bloom), drive the hive vitality to its maximum value of 2 within 3 weeks. This dynamic is described by the main reinforcing feedback loop R1 as presented in Figure 2.

Under base-case condition the feedback loop B1 as presented in Figure 2 is not active. The model runs show that the bees naturally manage their growth in a manner, that the brood does not exceed the brood rearing capacity.

When analysing the honey-stock dynamics over the simulation period (Figure 4) it is notable that the honey consumption increases while the colony initially declines. This behaviour can be explained with the comparatively high energy demand (honey consumption) of the increasing brood population. The honey stock continues to decline for about a month into the growth phase A, until the growing inflow, caused by an increasing forager cast size and food availability, surpasses consumption. This is a critical point in the colony development. The honey minimum must not fall below a threshold of 1,5 kg, under which starvation symptoms start to occur and deathrates increase, potentially causing the colony to collapse during the early growth phase.

During the saturation phase C net growth begins to slow down about 21 days (average development time from egg to hive-bee) after the queen reached her maximum egg-laying rate. At this point the colony growth is limited by the combined deathrates of all development stages, especially by the relatively high mortality of a growing forager population.

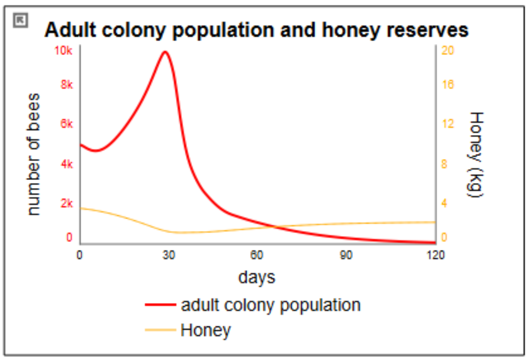
Failure Modes

In this subchapter I present the identified dynamic failure modes that can explain the colony failure behaviour as presented in the reference mode in Figure 1.

Starvation

The reference failure behaviour of case a) in Figure 1 qualitatively resembles simulation runs in which the honey stock was depleted, causing starvation. This was modelled by increasing deathrates for all development stages when the honey stock tends to zero.

A sensitivity analysis (APPENDIX) revealed that the colony development is highly sensitive to the initial colony conditions and the qualitative behaviour changes as soon as the values fall below certain tipping points. Keeping all other parameters at the values of the base- case, the colony shows the behavior presented in Figure 7 when the initial honey stock drops below the tipping point of 3,6 kg.



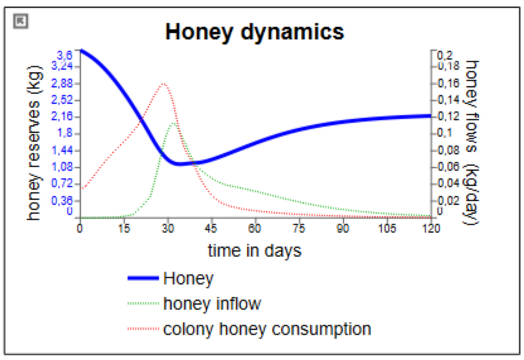


Figure 7: population (l) and honey (r) dynamics during a starvation event caused by low initial honey supplies

As previously described in the base-case *colony honey consumption* initially exceeds *honey inflow*, gradually depleting the stock (r). When it falls below a critical value of 1,5 kg starvation symptoms cause a rise in mortality rates (

Figure 8 (l)), which rapidly reduces the population (Figure 7 (l)), which in turn reduces the colonies honey consumption (Figure 7 (r)) and slows down the depletion of the stock. A decreasing colony size and honey inflow cause the hive vitality to drop to zero from which it cannot recover despite a continuing honey inflow, as the population dropped below the minimum strength of 3750 individuals (Becher et al., 2010, p. 775).

Figure 8 (r). The queen does therefore not resume egg-legging. The reinforcing loop of a decreasing population and *honey inflow* ultimately decreasing the queens *egg-laying rate* corresponds to the reinforcing feedback loop R1. The remaining foragers continue to gather nectar and the *honey stock* therefore slightly recovers to values above 1,5 kg, which decreases the deathrates back to normal levels

Figure 8 (l)). However, with no new bees in the making all remaining survivors slowly die off at their standard deathrates. In reality, predators and competing honeybee- colonies would invade a weakened hive, presumably leading to a premature total collapse. This could explain the relatively sharp population decline in the reference mode (Figure 1), compared to the simulation run.

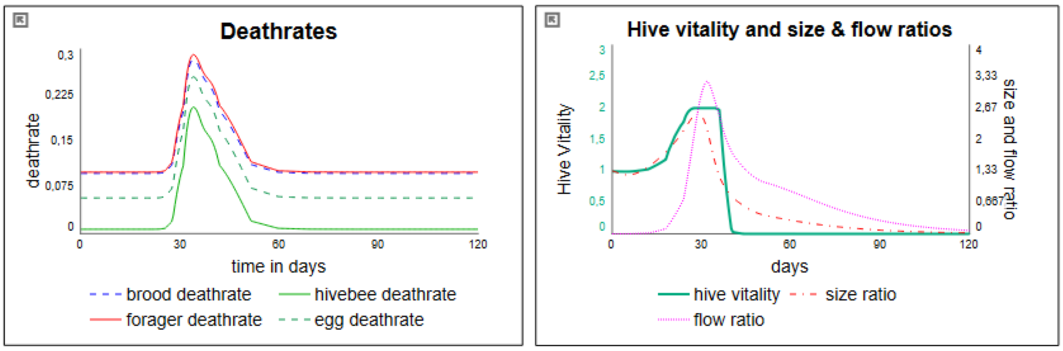


Figure 8: deathrates (l) and hive vitality (r) during starvation.

It is notable that, despite starvation losses, the *honey stoc*k does not turn to zero and even slightly recovers to about 2 kg during the simulation run. Beekeepers finding deserted colonies under inspection with remaining honey reserves (which is a common scenario) might therefore falsely exclude starvation as a plausible cause.

A similar dynamic behaviour and a starvation related collapse could be reproduced by limiting the average amount of flights per day (APPENDIX), which effectively limits the colonies honey supply. The parameter of *flights per day* is an exogenous factor and mainly defined by the local weather conditions. For the purpose of this model the average amount of flights per day over the simulation period is assumed to be constant and the value can be varied to investigate different seasonal flight scenarios. However, in reality this value would vary over the season depending on the local weather conditions. Under else identical base-case conditions, the tipping point was identified to be at an average of 4,2 flights per day over the simulated period. A lower flight rate will lead to starvation induced collapse.

Queen performance

The performed sensitivity analysis indicates that the overall qualitative population behaviour over time is sensitive to the queen's max egg laying capability. The indicated threshold for base-case conditions was identified to be 1320 eggs/day. If the queen's maximum capability falls below this rate the model generates the behaviour presented in Figure 9 for a maximum egg-laying rate of 1200 eggs/days. All other initial parameters correspond to the base-case setting.

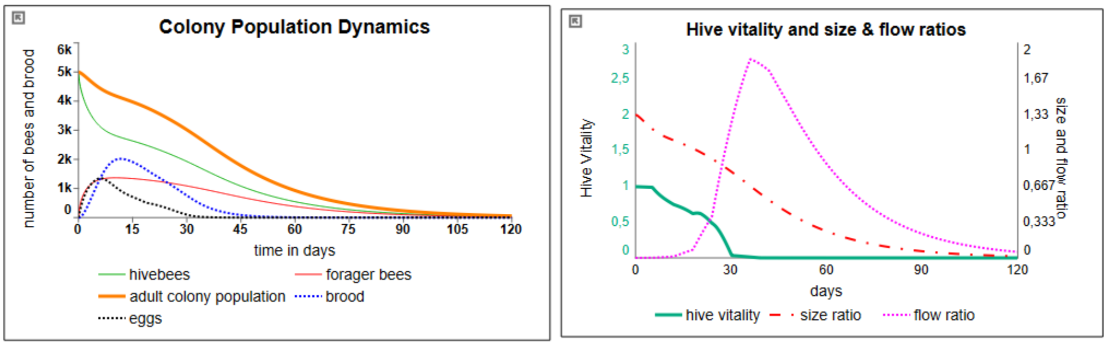
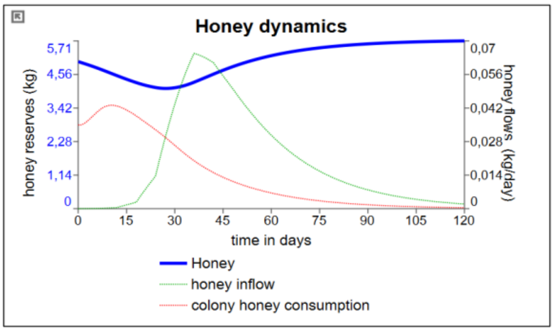


Figure 9: colony dynamics (l) and hive vitality(r) caused by an underperforming queen at a maximum rate of 1200 eggs/day

The colonies initial behaviour corresponds to phase A of the baseline case with a gradual population decline and an accelerated hive-bee- forager transition. The initial hive vitality of 1 in Figure 9 (r) triggers the queen to initiate egg-laying. But in contrary to the base-case the comparatively low production rate of new bees cannot make up for the overall mortality rate of the adult population, causing a gradual population decline. This has a negative impact on the hive vitality, which' decline can indeed be briefly halted by an increasing honey flow at ca. day 20, but this is ultimately not sufficient to prevent the declining hive size from undercutting the critical minimum size, driving the vitality to zero. This effectively halts egg-laying and therefore the resupply of new hive-bees to the stock (loop R1). As the foragers die at a higher standard mortality rate than the hive bees, their stock quickly gets depleted by its own mortality rate and a progressive resupply of the forager-bee stock (loop B2).



During this simulation run the *honey stock* continuously stayed above the critical level (

Figure 10) and increased mortality rates due to starvation symptoms can therefore be excluded from influencing the behavior presented in Figure 9. This case presents an explanation for the occasional observation of collapsed hives with significant amounts of food present in the colony.

Figure 10: Honey dynamics during poor queen performance (l)

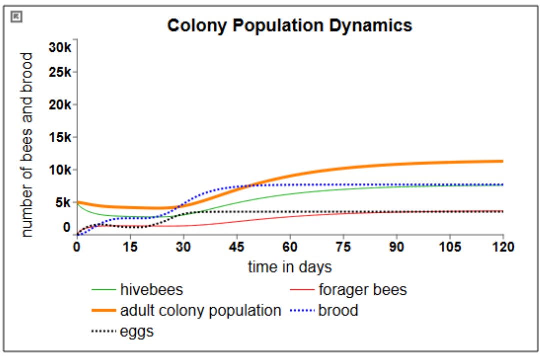


Figure 11: Colony development with a queen at max. 1400 eggs/day

The stagnating reference mode of behaviour b) as shown in Figure 1 (r) can be reproduced best by a simulation run featuring a poor performing queen with a maximum egg-laying rate of 1400 eggs/day (Figure 11). This value was identified as a tipping point under base-case conditions.

Forager Shock

External shocks could potentially disturb the internal dynamics of the colony and influence long term behaviour. As the hive itself is a hygienic well protected fortress the hive-bees and brood are relatively well protected from external factors. The foragers however leave the hive and are exposed factors negatively impacting their mortality rates.

A forager shock was implemented to simulate pesticide application and remove a certain amount of forager bees from the stock during the blooming period of the respective crop.

A sensitivity analysis was performed to investigate the mortality rate impact of a pesticide applied during the blooming period of the treated crop. The *start of crop-bloom* was set to day 30, corresponding to the blooming period of commercial plum trees. Figure 12 shows that the final population is not particularly sensitive to a loss of forager bees at various rates under base-case conditions.

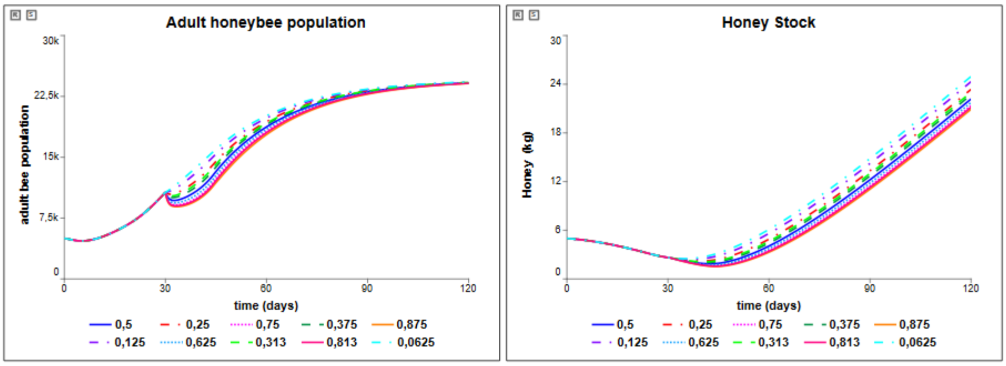


Figure 12: Colony (l) and Honey-stock (r) behaviour when exposed to pesticides with various mortality rates

Pesticide application causes a temporary dip in population, but this does not impact the long-term colony development (l). The honey stock is slightly affected with a difference of 4 kg between the most and least affected hive. But the qualitative behaviour is essentially unaffected. A strong colony with a solid honey stock is able to buffer the shock and recover.

As shown by the sensitivity analysis (Annex), the general qualitative behavior is however extremely sensitive to the initial hive conditions. A pesticide shock can cause severe consequences under circumstances slightly deviating from base-case conditions. This can be further explored in the interface section of the model. I will exemplarily present the shock response under identical conditions, but a slightly reduced initial honey stock of 4 kg, in Figure 13.

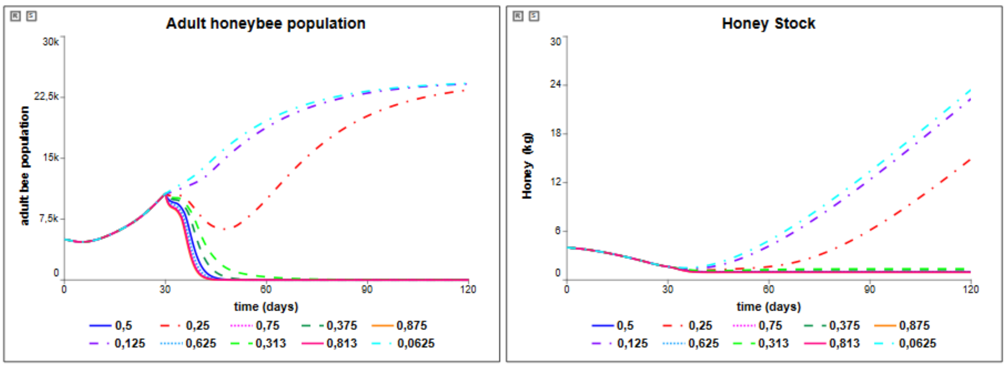


Figure 13: Colony (l) and Honey-stock (r) behaviour during various pesticide applications with 4 kg of initial honey

In this case the shock-response is sensitive to the mortality rate caused by the respective pesticide. While colonies exposed to pesticide mortalities of up to 0,25 successfully recover (l), colonies that have suffered losses beyond a certain threshold collapse. As shown in Figure 13 (r) the forager loss causes a depletion of the honey stock in line with the starvation behaviour described in the previous subchapter. The tipping point in this case was further identified at a critical pesticide mortality rate of 0,28.

At this point I would finally like to point out that identified values for the tipping points within this paper are not to be understood as general fixed values but depend on the respective colony conditions of the simulation run. The matrix of parameter combinations with varying values leads to a multitude of possible scenarios. Therefore, selected cases were chosen to present the general underlying dynamics.

5. Policy and limitations

Policies

The dynamics within the beehive are to a large degree governed by biology and are therefore very hard, if not impossible, to modify. However, a sensitivity analysis of key parameters showed that the colony is highly sensitive to the initial conditions of the colony, as well as to exogenous factors like weather (flights per day) and forager loss (pesticides). These provide potential leverage points to improve colony performance and can be addressed by improving beekeeping and farming practices.
Pesticide application should to a lager degree be coordinated with the beekeepers in order to minimize exposure, by e.g. making it mandatory to apply the substances during the night when most pollinators are inactive.

The beekeeping community today focusses on breeding higher performance queens to boost colony strength. But that seems to be only one part of the equation as forager lifetime turns out to be an important and sensitive factor limiting colony growth. Focussing on additional practices to boost forager lifetime and resilience, such as the provision of pollen supplements during bad weather periods (de Oliveira et al., 2020), could potentially have a substantial effect on colony strength.

The weather as such cannot be changed, however, sub-seasonal forecasts have improved in skill over the past decades and are breaching a usability barrier (Kushnir et al., 2019). Early information on e.g. below average temperatures for the upcoming month could predict a limited amount of flight days and hence nectar supply. This information could translate into the need for the beekeeper to artificially boost the hive vitality by simulating a nectar flow with the provision of sugar syrup, which increases the queen's egg-laying in time to reach the required forager numbers for sufficient pollination when the crop bloom starts. This practice would usually not be considered due to the additional costs for supply, time and equipment, but could turn out to be a profitable investment if the predicted sub-seasonal forecast realizes.

Limitations

The model represents a simplified honeybee colony model taking only the most basic and high level interaction dynamics into account. In reality the dynamics are incredibly complex and subject to ongoing research. The described feedback loops could be higher resolved and broken down into substructures, ultimately down to the level of a single bee.

I do not claim that the presented model is capable of predicting the development of an individual colony with given initial conditions. But it generates plausible and likely behaviour patterns. The main intention of the model structure was to explore how initial conditions, internal social dynamics and seasonal variables might interact to shape the overall behaviour over time, whilst still operating under minimal assumptions.

With the focus of the model and report being on the honeybee development, the farm sector is still at a very basic rudimentary stage. It requires further work to identify and implement further connections and influences between farming practices and the hive development.

Conclusion

A simple honeybee colony model has been developed to explore the inner dynamics shaping colony development. The behavior is very sensitive to initial conditions and exogenous factors such as weather conditions. Relevant tipping points have been identified for the base-case scenario.

The reference mode of behaviour, both for thriving and collapsing colonies could be reproduced.
Three different plausible failure modes, starvation, queen performance and forager loss have been

identified and presented.

Despite the models limitations it fulfills its purpose of serving as a pedagogical tool for beekeepers and farmers to highlight and visualize the importance of key parameters and shocks on the overall honeybee-colony and pollination performance. It can be further extended beyond its initial purpose by adding further biology driven behavioral dynamics and taking additional endogenous and exogenous factors of interest into account.

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ANNEX

Sensitivity Analysis of initial conditions

Initial Honey Supply

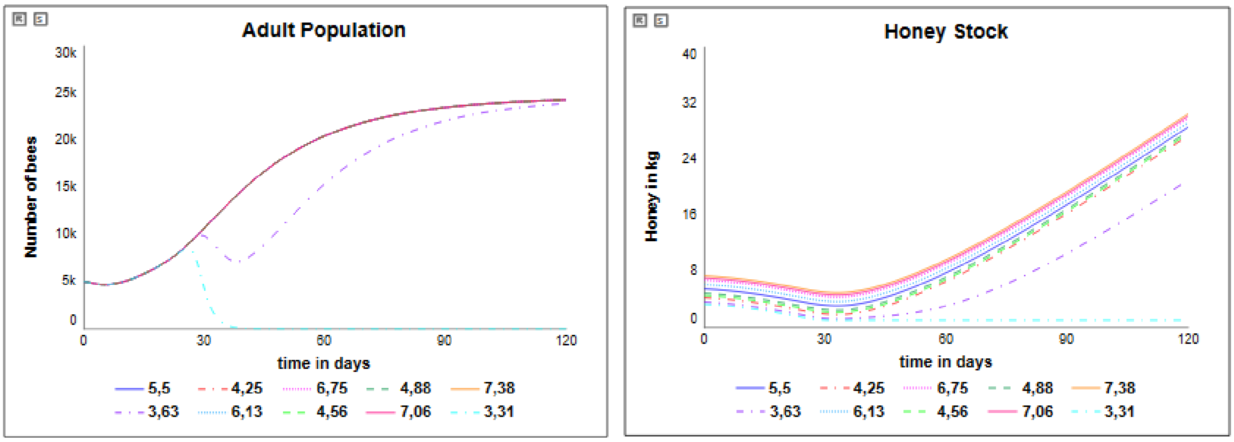


Figure 14: init_hone: 3-8 kg, base-case conditions, , uniform distribution, 10 runs

Initial Colony Strength

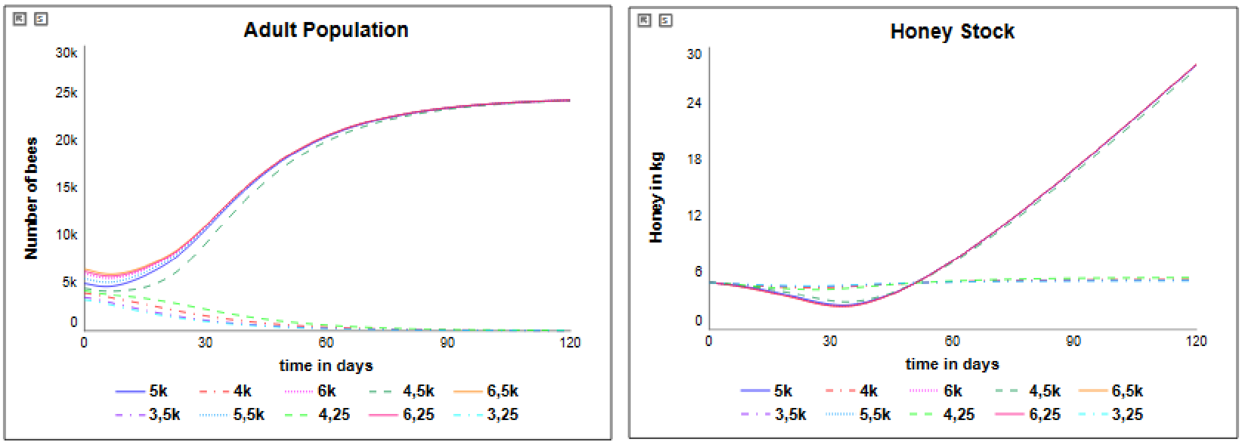


Figure 15: init_hivebees: 3000-7000, base-case conditions, , uniform distribution, 10 runs

Queen Performance

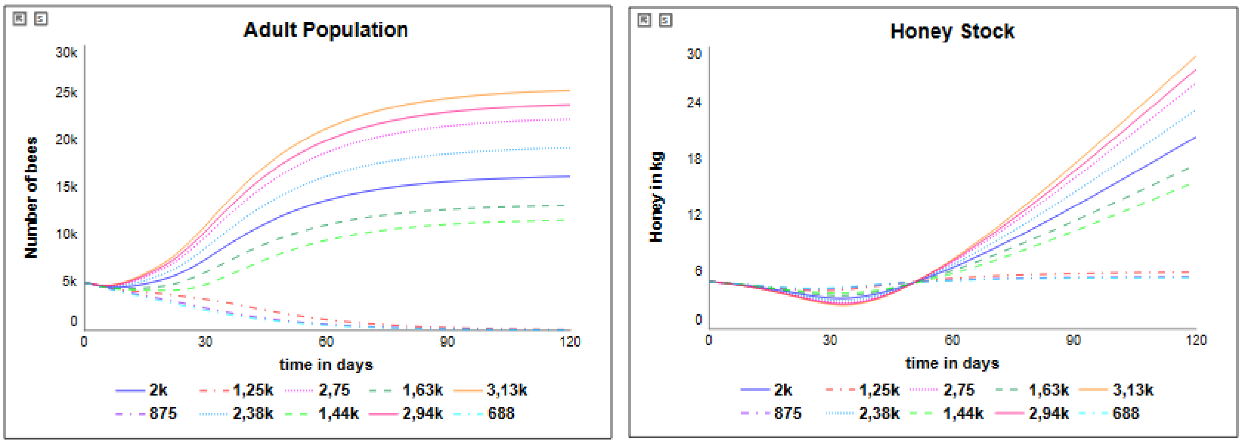


Figure 16: max_eggs_per_day: 500-3500 , base-case conditions, uniform distribution, 10 runs

Flight conditions

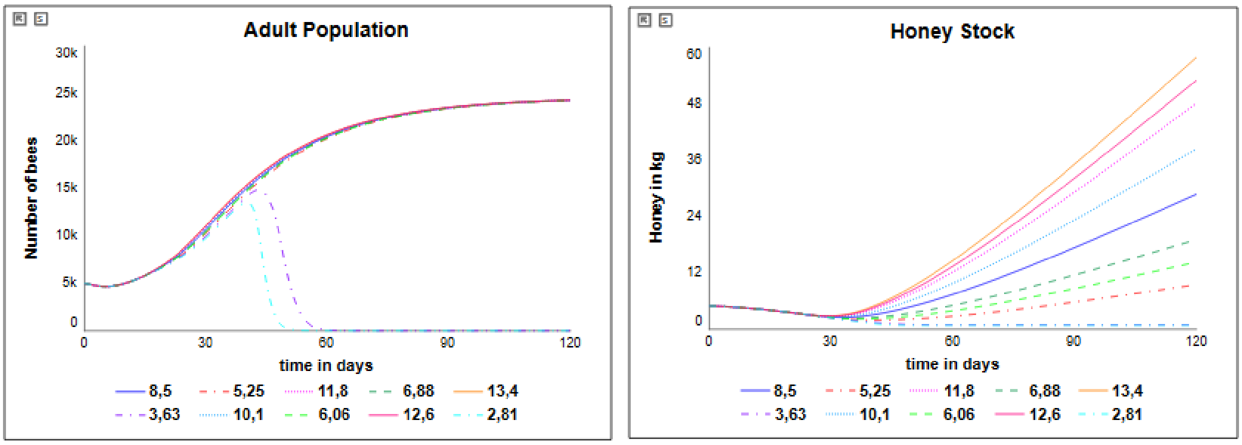
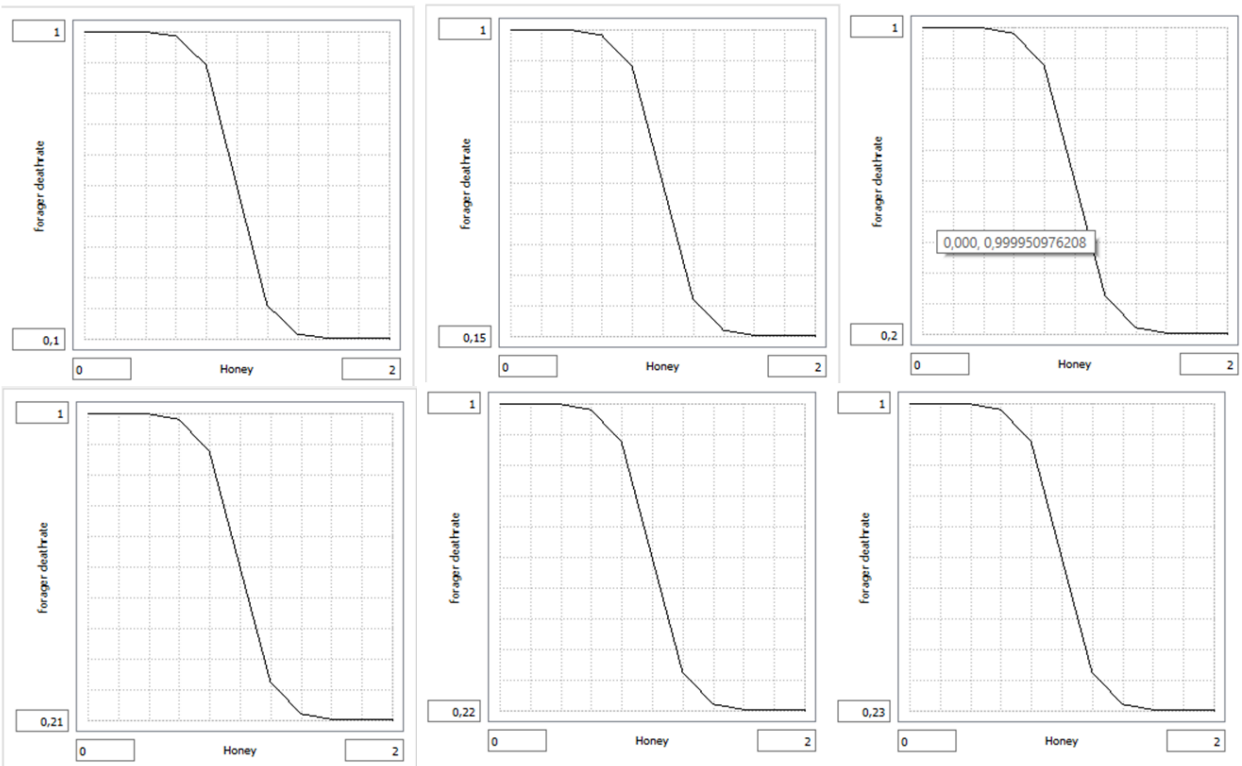


Figure 17: flights_per_day: 2-15, base-case conditions, uniform distribution, 10 runs

The performed analysis reveals a high sensitivity to the initial conditions under else base-case parameter values.

Standard forager mortality rate

The standard forager mortality rate has been varied from 0,1 (base-case) to0,23 according to the following graphs.



The corresponding responses are shown in the figures 18-13 below.

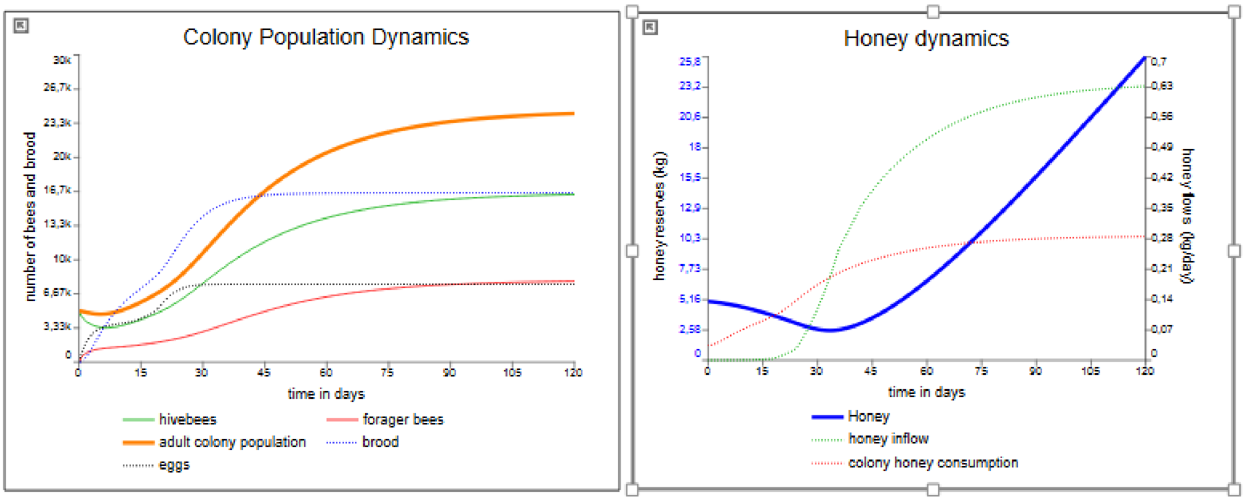


Figure 18: Colony and honey dynamics under base-case conditions and standard forager mortality rate of 0,1

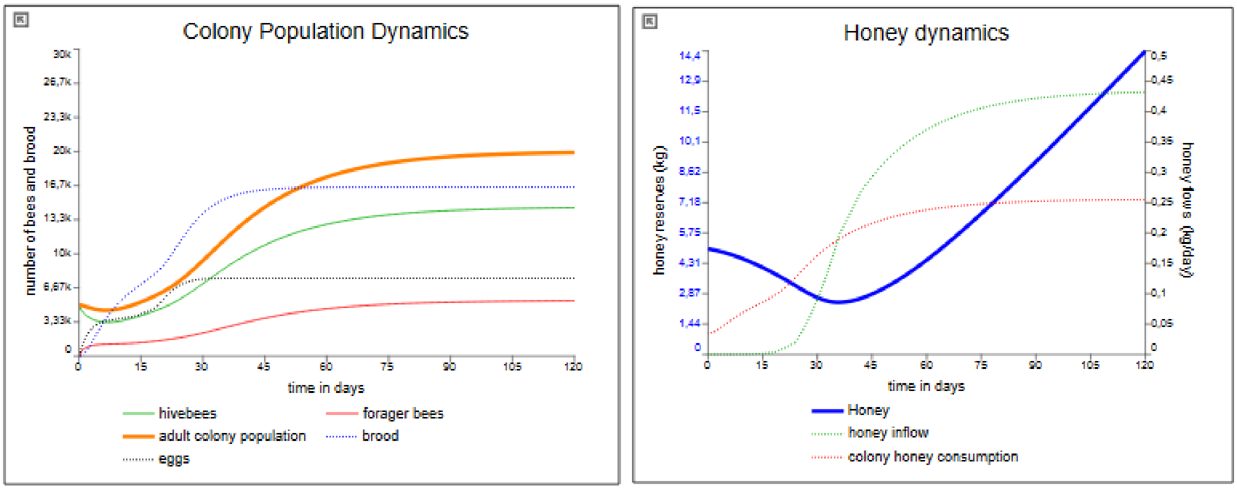


Figure 19: Colony and honey dynamics under base-case conditions and standard forager mortality rate of 0,15

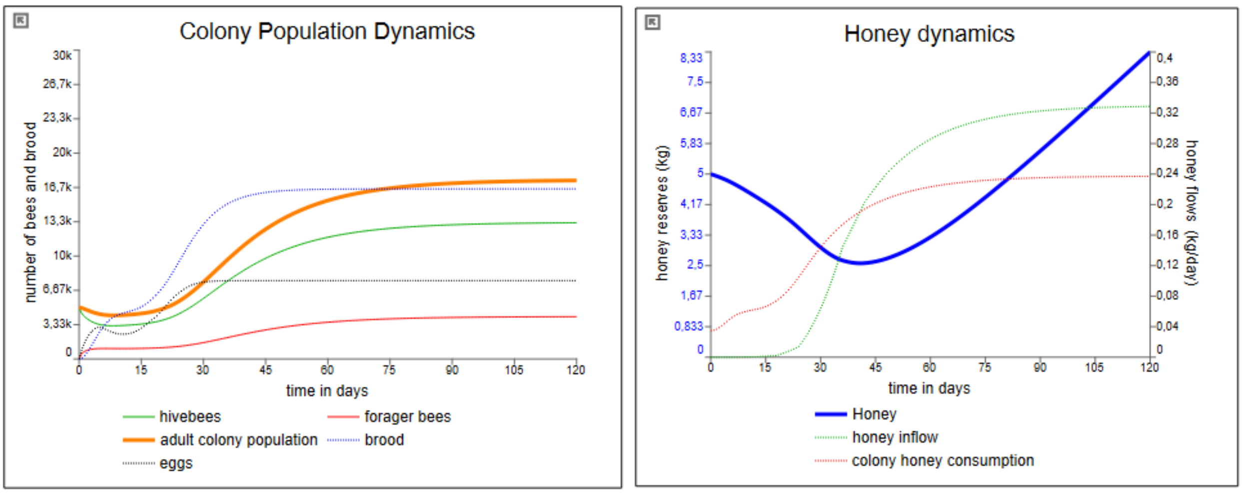


Figure 20: Colony and honey dynamics under base-case conditions and standard forager mortality rate of 0,2

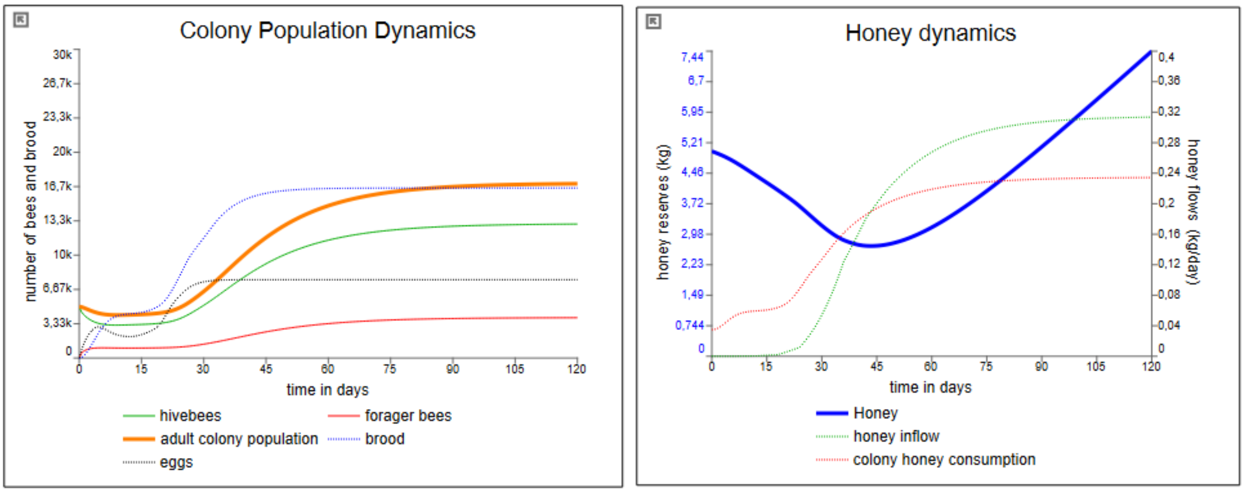


Figure 21: Colony and honey dynamics under base-case conditions and standard forager mortality rate of 0,21

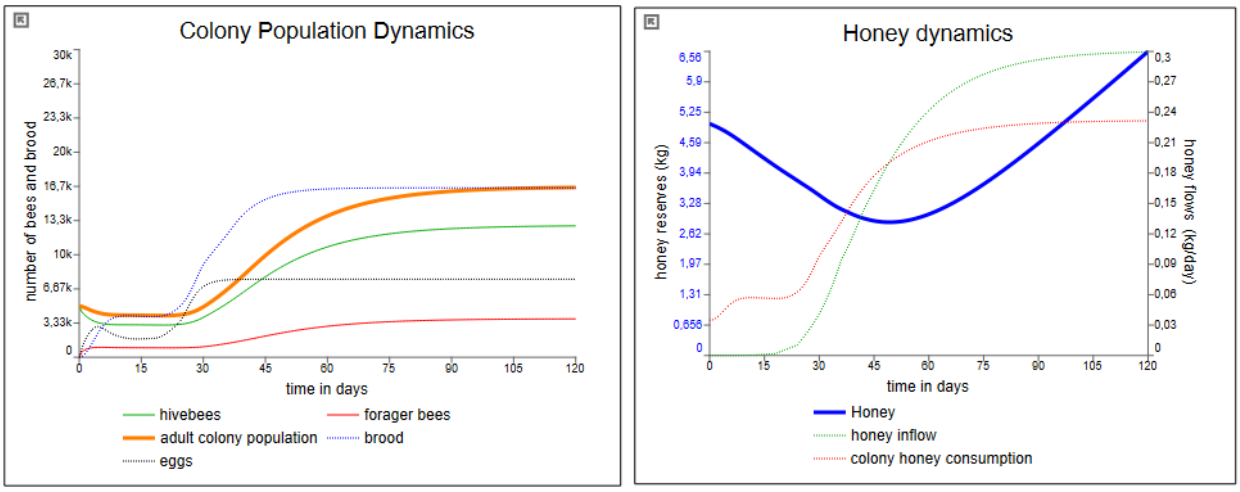


Figure 22: Colony and honey dynamics under base-case conditions and standard forager mortality rate of 0,22

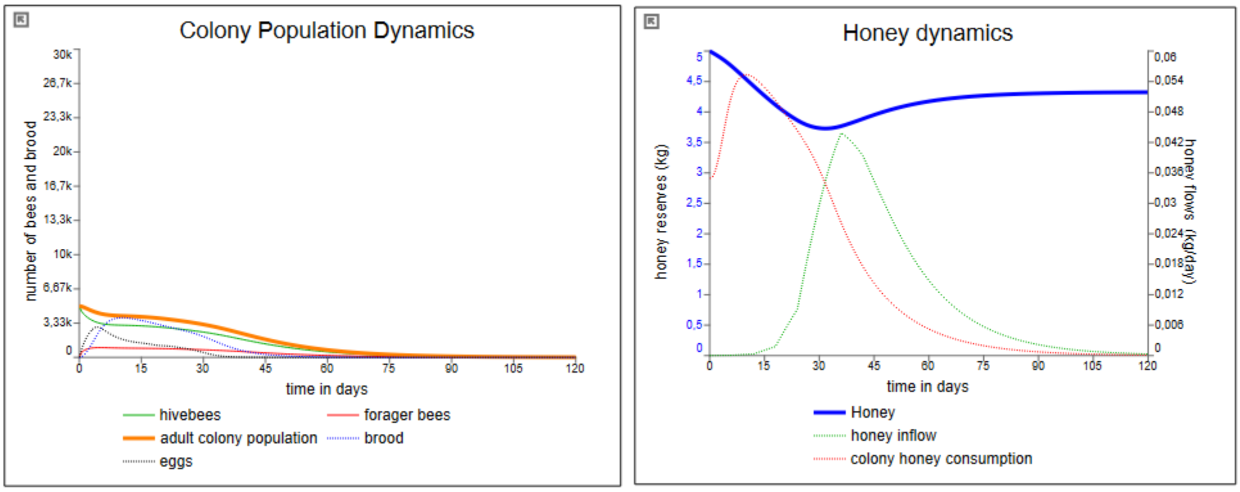


Figure 23: Colony and honey dynamics under base-case conditions and standard forager mortality rate of 0,23

The analysis revealed a high sensitivity to the standard forager mortality rate. A tipping point of 0,22 was identified. Meaning a colony suffering from a forager loss exceeding 22%/day under else base-case conditions is not able to maintain a stable population.

Additional Assumptions

- Drones are not considered
- Linear social inhibition relation
- No diseases present in the colony
- No Varroa mites present in the colony
- Food consists of pollen and nectar
- A minimum of 10% of hive-bees are required to perform jobs other than rearing brood
- Different brood stages are not considered
- Average amount of flight days is constant throughout the simulation period
- No beekeeper intervention during the simulation period
- One bee-hive per fruit farm
- Baseline death-rates for all stages are considered constant over the simulation period
- The amount of honey per flight is assumed constant over the simulation period
- Food consumption rates are considered considered constant over the simulation period
- Death-rates start increasing due to low supplies below 1,5 kg
- Honey inflow and colony size have equal weights in influencing hive vitality
- Pesticide effect is 100% on first day of application and linearly declines over blooming period

Base-case Scenario Documentation

Software: Stella Architect 2.14
Integration method: Euler
Time Unit: days
Simulation start time: 0
Simulation end time: 120

The base-case scenario represents the normal behaviour of a strong and healthy hive under steady state conditions

Init_hivebee: 5000
Init_honey: 5
Max_eggs_per_day: 3000
Flights_per_day: 8

Number_of_trees: 5000
Start_of _crop_bloom: 30
Blooming_period: 10
Pollination_visitation_rate: 5
Flowers_per_tree: 200

Pesticide_switch: off

Max_persticide_mortality: 0,9

	Equation	Properties	Units	Documentation	Annotation
Top-Level Model:					
brood(t)	brood(t - dt) + (hatching_eggs - broodloss_due_to_hivebee_capacity - dying_brood - hatching_bees) * dt	INIT brood = 0	bee	The amount of brood in the hive. The initial value is zero, as there is no brood present before the queen starts laying eggs. Larva hatches from the eggs. The time span for the larva to develop into an adult bee is called brood phase. In this model I do not differentiate between different stages of brood (larva, pupa, capped brood).	
eggs(t)	eggs(t - dt) + (eggs_laid - hatching_eggs - dying_eggs) * dt	INIT eggs = 0	bee	The amount of eggs currently in the colony. The initial amount is zero as there are no eggs present before the queen starts laying eggs.	
forager_bees(t)	forager_bees(t - dt) + (forager_recruitment - dying_foragers - killed_foragers) * dt	INIT forager_bees = 0	bee	The amount of forager bees in the hive. Forager bees leave the hive to forage and are responsible for providing energy (food) to the colony. The initial value is zero, as there are no foragers present before the foraging season starts in spring.	
hivebees(t)	hivebees(t - dt) + (hatching_bees - forager_recruitment - dying_hivebees) * dt	INIT hivebees = init_hivebee	bee	Amount of hive-bees present in the hive. The initial value corresponds to the amount of bees that survived winter (init_hivebee). Bees spend the first part of their life as hive-bees. Hive-bees have jobs inside the hive and do not leave it. The main responsibility is rearing the brood, but also includes jobs such as building honeycomb, cleaning, guarding, honey processing and ventilating. The amount of time the bees spend as hive-bees varies depending on the demography of the hive.	
Honey(t)	Honey(t - dt) + (honey_inflow - colony_honey_consumption) * dt	INIT Honey = init_honey	kg	Amount of honey stored in the hive (kg). The initial value corresponds to the reserves that the bees have in the colony when the breeding season starts. This can be leftovers from the winter reserves or a resupply provided by the beekeeper before the season.	
total_amount_of_pollinated_flowers(t)	total_amount_of_pollinated_flowers(t - dt) + (pollination_per_day) * dt	INIT total_amount_of_pollinated_flowers = 0	flowers	flowers pollinated by bees within the simulation period	
total_amount_of_pollinated_fruit_flowers(t)	total_amount_of_pollinated_fruit_flowers(t - dt) + (fruit_pollination_per_day) * dt	INIT total_amount_of_pollinated_fruit_flowers = 0	flowers	Total amount of pollinated fruit flowers.	

broodloss_due_to_hivebee_capacity	MAX ((brood-max_brood_rearing_capacity)/TIME_TO_DIE_:O; 0)		bee/days	The amount of brood lost per day when the total amount exceeds the maximal brood rearing capacity of the hive bees.	UNIFLOW
colony_honey_consumption	MIN ((Honey/TIME_TO_CONSUME_HONEY); ((hivebees*HIVEBEE_CONSUMPTION)+(brood*BROOD_CONSUMPTION)+(forager_bees*FORAGER_CONSUMPTION)))		kg/days	Total colony honey consumptiom. It is used to feed brood, hivebees and forager bees and heat up the hive (by muscle activity)	
dying_brood	(brood*brood_deathrate)/TIME_TO_DIE_:O		bee/days	The amount of brood dying per day.	UNIFLOW
dying_eggs	(eggs*egg_deathrate)/TIME_TO_DIE_:O		bee/day	the amount of eggs dying per day.	
dying_foragers	forager_bees*forager_deathrate/TIME_TO_DIE_:O		bee/days	Forager dying per day.	UNIFLOW
dying_hivebees	hivebees*hivebee_deathrate/TIME_TO_DIE_:O		bee/days	The number of hive-bees dying per day.	UNIFLOW
eggs_laid	egg_laying_rate*max_eggs_per_day		bee/days	The amount of eggs laid per day depending on factors such as season, hive strength and honey inflow.	UNIFLOW
forager_recruitment	hivebees/hivebee_transition_age		bee/days	After a certain amount of time, depending on the amount of foragers already present in the hive and the amount of brood to take care of, hive-bees get recruited to become forager bees. The minimum time as a hive-bee before becoming a forager bee is 4 days due to physiological reasons. The average time spent as a hive-bee typically is 21 days. One hive bee can take care of max 3 brood cells. Therefore a minimum amount of 1/3 of the brood-cells must be present as hive-bees, otherwise the death-rate of brood will increase accordingly.	
fruit_pollination_per_day	IF TIME >start_of_crop_bloom AND TIME< start_of_crop_bloom+blooming_period THEN flowers_visited_per_flight*total_successful_flights_per_day ELSE 0		flowers/days	The number of visited flowers within a certain time range, defined by the blooming period.	
hatching_bees	brood/BROOD_TIME		bee/days	bees hatch after being brood for 18 days (21 days after the egg was laid)	UNIFLOW
hatching_eggs	eggs/HATCHING_TIME		bee/days	The amount of eggs hatching per day.	UNIFLOW
honey_inflow	total_successful_flights_per_day*honey_per_successful_flight		kg/day	honey flow into the hive per day dependent on amount of total flights and average amount of honey per flight.	
killed_foragers	IF pesticide_switch=1 AND TIME >= start_of_crop_bloom AND TIME <=start_of_crop_bloom+blooming_period THEN max_pesticide_mortality*(1-((TIME-start_of_crop_bloom)/blooming_period))*forager_bees ELSE 0		bee/days	Foragers killed in the field in case of pesticide application. Pesticide is applied on the first day of the crop bloom. The application has the maximum effect on day 1 but the effect gradually wears down to the end of the blooming period. This is an assumption, as the effect of pesticides over time is poorly	UNIFLOW

				documented, In the literature usually average values are given for the mortality over a certain period of time.	
pollination_per_day	flowers_visited_per_flight*total_successful_flights_per_day		flowers/days	Amount of total flowers visited per day	
adult_colony_population	hivebees+forager_bees		bee	The adult colony bee population is the amount of hive-bees + the amount of forager bees.	
blooming_period	10		day	The time that the crop is in bloom.	
BROOD_CONSUMPTION	0,000007		kg/(bee*day)	Honey consumed per brood cell per day. (Khoury, 2013, p. 3)	
brood_deathrate	GRAPH(Honey) Points: (0,000, 1,0000), (0,200, 1,0000), (0,400, 0,998136332664), (0,600, 0,985581666795), (0,800, 0,898032661275), (1,000, 0,5490), (1,200, 0,199967338725), (1,400, 0,112418333205), (1,600, 0,0998636673361), (1,800, 0,0982379607989), (2,000, 0,0980303360316)		dmnl	The rate at which the brood is dying. The standard combined brood death-rate was observed to be 9,8% in a healthy colony. (Fukuda & Sakagami, 1968, p. 34) Brood has a high energy demand in the growth phase. Brood dies when this energy demand is not met and in addition brood is cannibalized by hive-bees when the colony runs out of honey supplies. If the honey stock drops below 2 kg the colony starts to show stress behavior and below 1,5 kg first starvation symptoms appear due to local food supply insufficiencies.	
BROOD_PER_HIVEBEE	2,5		bee/bee	The amount of brood cells that one nurse-bee can take off. This value ranges from 2.3 to 3 in the literature (Torres et al., 2015, p. 8) The base-case value is set to 2,5.	
BROOD_TIME	18		day		
egg_deathrate	GRAPH(Honey) Points: (0,000, 0,999961304649), (0,200, 0,999708380191), (0,400, 0,997806115769), (0,600, 0,983709846511), (0,800, 0,889673910595), (1,000, 0,5290), (1,200, 0,168326089405), (1,400, 0,0742901534889), (1,600, 0,0601938842308), (1,800, 0,0582916198092), (2,000, 0,0580386953514)		dmnl	The rate at which eggs are dying. The standard egg death rate corresponds to the normal rate of loss in a healthy colony. 5,8% according to (Fukuda 1986, p. 34) According to practical beekeeping wisdom and observations a colony should always have a minimum amount of 2 kg in the hive. Below that the hive begins to show stress behaviour and deathrates rapidly increase below 1 kg due to local insufficiencies and distribution issues. The bees will start to cannibalize the eggs to save resources and the deathrate quickly rises to 1.	
egg_laying_rate	GRAPH(hive_vitality) Points: (0,000, 0,000), (0,200, 0,0179862099621), (0,400, 0,0474258731776), (0,600, 0,119202922022), (0,800, 0,26894142137), (1,000, 0,500), (1,200, 0,73105857863), (1,400, 0,880797077978), (1,600, 0,952574126822), (1,800, 0,982013790038), (2,000, 0,993307149076)		dmnl		

flights_per_day	8		flight/(day*bee)	The number of average flights a forager bee does per day. Under natural foraging conditions, the mean numbers of trips per day by workers range from 1 to 13.5, (Rodney & Purdy, 2020, p. 167) The value strongly depends on the local flight (weather) conditions.	
flow_effect	GRAPH(flow_ratio) Points: (0,000, 0,000), (0,200, 0,33583091167), (0,400, 0,560945103841), (0,600, 0,7118436595), (0,800, 0,812993986277), (1,000, 0,880797077978), (1,200, 0,926246849528), (1,400, 0,956712742486), (1,600, 0,977134641257), (1,800, 0,99082384938), (2,000, 1,000)		dmnl	The flow effect can take values from 0-1 following an saturation function based on the flow ratio. At a flow ratio of zero the flow effect is zero. With an increasing flow ratio the flow effect quickly increases. The impact of an increasing flow is higher at low levels and decreases at higher levels, saturating at 1. This corresponds to observed behavior.	
flow_ratio	honey_inflow/inflow_threshhold		dmnl	The ratio of the inflow threshold and honey inflow. An increasing honey flow, as a sign of spring, triggers the queen to increase egg-laying. The threshold is chosen to be the ratio of inflow to initial consumption. When the flow exceeds the consumption and the honey stock increased the queen increased her egg laying rate.	
flowers_per_tree	200		flowers/tree	The average amount of flowers per crop tree, depending on tree-species, age and annual variation.	
flowers_visited_per_flight	50		flowers/flight	amount of flowers a bee visits per flight	
food_availability	GRAPH(spring_season) Points: (0,00, 0,00011165334063), (6,00, 0,000688710914073), (12,00, 0,00423553964084), (18,00, 0,025580788312), (24,00, 0,139433872962), (30,00, 0,500), (36,00, 0,860566127038), (42,00, 0,974419211688), (48,00, 0,995764460359), (54,00, 0,999311289086), (60,00, 0,999888346659)		dmnl	The potential food availability within the flight radius (3 km) of the beehive depending on time (season) and local flora. The potential food availability depends on the time in the season and is defined by the blooming periods of various nectar providing plants. The shape of the S-function is based on records and experience from a local bee-keeper and representative of the Bergen Beekeeping association (Manuel Hempel). During the first 30 days (typically march in Bergen) the local flora provides very little nectar. Beginning with a low nectar availability from spring flowers (crocus, daffodils) the supply quickly increases once the willow trees start blooming all at once at the end of march/early Mai (day 30). When spring kicks in and temperatures rise above 12C a multitude of flowers simultaneously starts blooming, rapidly increasing food availability. The potential food availability is thereafter stabile at a high level as a continuous bloom of blueberries, dandelions, clover, fruit trees (agricultural relevance) and wild raspberries provides the basis for a high number of successful flights.	

FORAGER_CONSUMPTION	0,000007		kg/(bee*day)	Honey consumed per hivebee per day. 0,007 g according to (Harbo, 1986)	
forager_deathrate	GRAPH(Honey) Points: (0,000, 1,0000), (0,200, 1,0000), (0,400, 0,998350354952), (0,600, 0,986703371476), (0,800, 0,901812860924), (1,000, 0,5500), (1,200, 0,198187139076), (1,400, 0,113296628524), (1,600, 0,101649645048), (1,800, 0,100202335093), (2,000, 0,100024782122)		dmnl	The rate at which forager bees die. Forager bees have a high risk of death (predators, rain, getting lost, pathogens) and usually die at a rate of about 10% per day (Dukas, 2008, p. 253) As summer bees have low internal reserves (Keller et al., 2005, p. 7) and a high energy demand due to flying activity. If the honey stock drops below 2 kg the colony starts to show stress behavior and below 1,5 kg first starvation symptoms appear due to local food supply insufficiencies. It is assumed that they die within a day without food and the death-rate increases to 1.	
forager_fraction	forager_bees/(hivebees+forager_bees)		dmnl	Percentage of foragers of total colony population.	
HATCHING_TIME	3		day	The time it takes for an egg to hatch, which is 3 days. (Wu et al., 2011, p. 6)	
hive_vitality	(size_effect*weight_size)*((flow_effect*weight_flow)+1)		dmnl	The vitality of the hive influences the queen egg-.laying behavior. Increasing vitality (honey inflow and colony growth) increases egg-laying performance. A multiplication is chosen as the term needs to become zero when the size effect is 0 (no bees, no egg laying). However, a colony at certain strength will continue laying eggs, even if there is no flow, but sufficient honey stock in the hive. In the case of zero flow the hive size is dominant and the right size of the equation turns to one.	
HIVEBEE_CONSUMPTION	0,000007		kg/(bee*day)	Honey consumed per hive-bee per day. 0,007 g according to (Harbo, 1986)	
hivebee_deathrate	GRAPH(Honey) Points: (0,000, 1,0000), (0,200, 1,0000), (0,400, 0,99838537403), (0,600, 0,986441916516), (0,800, 0,895467496204), (1,000, 0,5035), (1,200, 0,111532503796), (1,400, 0,0205580834837), (1,600, 0,00861462597049), (1,800, 0,00719024150464), (2,000, 0,00702238661864)		dmnl	The death rate of hive-bees depends on the honey-storage situation in the hive. Hive-bees are well protected inside the hive and therefore die at relatively low rates of about 0,7%) (Russell et al., 2013, p. 167) As summer bees have low internal energy reserves within their bodies (Keller 2015, p.7) they require a continuous energy supply. It is assumed that they die within a day without food.	
hivebee_transition_age	MINIMUM_HIVEBEE_TIME+(transition_factor*forager_fraction)		day	Time a bee spends as a hive-bee before turning into a forager bee. In a typical healthy colony the percentage of foragers of the total population is about 33% and the time spent as a hive-bee before transitioning to a forager bee is 21 days (Fukuda & Sakagami, 1968,	

				p. 33). But there is a feedback loop called "social inhibition" that regulates the amount of hive-bees in a colony. If there are no foragers in the colony at all, the colony desperately needs foragers to secure the honey supply. In that case hive bees are recruited earlier than usual to become foragers. The youngest age at which they can physically transition is 4 days (Fahrbach & Robinson, 1996, p. 1). So if there are 0 foragers in the colony a certain fraction of hive-bees become foragers after 4 days. If the amount of foragers in a colony exceeds 33% there are more than enough foragers available so the recruitment of new foragers from the hive-bee stock is delayed. I therefore came up with the stated formula, based on the transition times of 4 days at 0% foragers and 21 days at 33% foragers. A linear relationship is assumed. The formula reduces the standard forager recruitment of 21 days if there are less than 33% of foragers presents and extends the transition time beyond 21 days if the percentage rises above 33%.	
honey_per_successful_flight	0,00001		kg/flight	This is the average amount of honey a bee brings in per flight. According to (Harbo 1986) a forager can gather up to 100 mg of honey per day. With up to 10 successful flights per day (as stated by (Van der Steen, 2015) this results in 10 mg/flight	
inflow_threshhold	init_hivebee*HIVEBEE_CONSUMPTION		kg/day	the threshold is the value corresponding to when the inflow gets larger than the initial consumption based on the initial population.	
init_hivebee	5000		bee	The initial amount of bees in the colony after winter. The initial hive-bee value represents the amount of bees in the hive that have survived winter. This is the starting population in spring. The value is based on personal experience and ranges between 5000 and 10000.	
init_honey	5		kg	The initial amount of food reserves the colony has at the beginning of the season. This can either be excess honey from winter supplies or food supplied by the beekeeper.	
max_brood_rearing_capacit y	hivebees*BROOD_PER_HIVEBEE*MAXIMUM_SHARE_OF_NURSEBEES		bee	One hivebee can take care of max amount of brood cells. The hive-bee stock therefore balances the max. amount of brood that can be raised at the same time.	
max_eggs_per_day	3000		bee/day	This is the maximum amount of eggs the queen lays per day. depending on the queen this ranges between 1500 and 3000 eggs per day. (Wei 2019, p.1)	
max_pesticide_mortality	0,9		dmnl/days	The forager bee mortality caused by the applied pesticide. Even though pollinators are not deliberately targeted by the	

				pesticides, their application is proven to have dramatic effects on the survival rate of exposed forager bees. (Calatayud-Vernich et al., 2019, p. 1). The mortality depends on the type of pesticide, application strategy and duration of exposure.	
MAXIMUM_SHARE_OF_NURSEBEES	0,9		dmnl	Nurse-bees are the subgroup of the hive-bees that raise the brood. This parameter defines the maximum share of nurse-bees of the overall hive-bees. The normal ratio is about 2/3 (Johnson, 2010, p. 306). It is assumed that the rate can rise to 90% under extreme conditions. Not all hive-bees are available for brood rearing. A minimum amount needs to be taking care of other responsibilities to guarantee the functioning of the colony (building comb, ventilating, guarding the entrance etc.)	
MINIMUM_HIVEBEE_TIME	4		day	The minimum time a bee must spend as a hive-bee before transitioning to a forager bee is 4 days (Fahrbach 1996, p.1)	
minimum_strength	3750		bee	If the adult colony population drops below this value the hive is too weak to produce sufficient heating power to produce and raise brood. The queen stops laying eggs when the colony strength drops below the value of 3750. (Becher et al., 2010, p. 775)	
number_of_trees	5000		tree	The amount of crop trees within the bees flight radius	
pesticide_switch	0		dmnl	Switch to activate (1) or deactivate (0) pesticide application. Pesticides are commonly only applied once during the blooming period. In this model the pesticide is applied on day 1 of the blooming period.	
pollination_rate	total_amount_of_pollinated_fruit_flowers/(flowers_per_tree*number_of_trees*Pollinator_visitation_rate)		Dimensionless	The pollination rate indicates sufficient pollination depending on the flowers per tree, number of trees in the orchard. A value of 1 indicates sufficient pollination. If it is not met, more beehives are required.	
Pollinator_visitation_rate	5		dmnl	Number of times a flower needs to be visited by a pollinator for sufficient pollination. The number depends on the crop. For apples it is around 5 visits per flower. (Garrat 2016, p.7)	
size_effect	GRAPH(size_ratio) Points: (0,000, 0,000), (0,200, 9,21359998566e-8), (0,400, 0,00000528834461462), (0,600, 0,000303447030029), (0,800, 0,0171240333157), (1,000, 0,500), (1,200, 0,982875966684), (1,400, 1,000), (1,600, 1,000), (1,800, 1,000), (2,000, 1,000)		dmnl	The size effect can take values from 0-1 following an S-shaped function based on ratio size. for a size ratio <1 the population size is below the minimum required hive strength. The queen will not lay eggs, as the colony is too weak to provide sufficient heating. The effect quickly grows to one when the the size ratio passes one. This corresponds to observed behavior.	

size_ratio	adult_colony_population/minimum_strength		dmnl	The colony growth is a trigger that encourages the queen to lay more eggs. The initial hive bee population is therefore used as the reference.	
spring_season	TIME		day	The 120 day period of interest starting from early spring. This corresponds to the running time of the model.	
start_of_crop_bloom	30		day	The day the crops start to bloom.	
TIME_TO_CONSUME_HONEY	1		day	Time it takes the bees to consume the honey	
TIME_TO_DIE_:O	1		day	the deathrate corresponds to a time frame of 1 day	
total_successful_flights_per_day	forager_bees*food_availability*flights_per_day		flight/day	The total amount of successful flights per day, depending on the flights per day and the food/flower availability.	
transition_factor	51		day	Slope in linear part of hivebee time equation. This value is chosen for a linear fit through the data points of 4 days / 0%foragers and 21 days / 33% foragers.	
weight_flow	1		dmnl	The weight of the flow effect on hive vitality. Its is assumed that the size and the flow have equal weight in affecting the hive vitality, which corresponds to established practical beekeeping knowledge. The evidence is anecdotal and a literature review could neither confirm nor deny this assumption.	
weight_size	1		dmnl	The weight of the size effect on hive vitality	

Total	Count	Including Array Elements
Variables	77	77
Modules	1	
Sectors	7	
Stocks	7	7
Flows	14	14
Converters	56	56
Constants	37	37
Equations	33	33
Graphicals	8	8

Run Specs	
Start Time	0
Stop Time	120
DT	1/4
Fractional DT	True
Save Interval	0,25
Sim Duration	1,5
Time Units	days
Pause Interval	0
Integration Method	Euler
Keep all variable results	True
Run By	Run
Calculate loop dominance information	True
Exhaustive Search Threshold	1000