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Research Article

Food for thought: could the queen's egg-laying rate in the BEEHAVE honey bee model emerge from the effects of brood pheromones, weather conditions, and pollen availability?

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Abstract

The BEEHAVE honey bee model is widely recognised for its ability to analyse the impact of local land use, including pesticide use, weather conditions, mite infestations, and beekeeping practices, on the risk of colony loss. However, it is based on an imposed egg-laying rate that represents only average conditions in Central Europe while also being the main driving factor in colony dynamics. A modified version of the model, called BEEHAVE-PPE (Pollen Pheromone Egg-laying), was developed, in which positive feedback between pollen foraging and the egg-laying rate was implemented. It was assumed that daily pollen foraging depends not only on weather conditions but also on brood size, brood pheromones, and temperature. The six parameters of the new BEEHAVE-PPE module were calibrated using demographic and weather data from a bee colony monitoring area in France. This produced realistic colony dynamics under average weather conditions but not under prolonged periods of adverse weather that prevented foraging. Although the model is based on unverified heuristic assumptions regarding brood pheromone production and dynamics, the results suggest that it is plausible that the egg-laying rate in honey bee colonies is influenced by local weather conditions and feedback from the brood. The new version, BEEHAVE-PPE, is not intended for direct use but rather to stimulate empirical research on queen egg-laying, brood pheromone signalling, and theoretical work on colony feedback dynamics.

Key words: BEEHAVE, brood pheromones, egg-laying, emergence, honey bees, multiple stressors, pollen storage

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Introduction

The Western honey bee (*Apis mellifera*) is exposed to various stressors, including pesticide exposure, parasites, predators, and reduced forage availability due to prolonged adverse weather conditions or monoculture farming. The resulting increase in honey bee colony mortality (Potts et al. 2016; Henry et al. 2017; Requier et al. 2019) is thought to be due to the cumulative impact of these stressors acting together. However, traditional empirical

laboratory approaches are limited in their ability to analyse such combinations (Henry et al. 2017). Realistic computational models can overcome these limitations by testing scenarios involving single or multiple stressors affecting a colony (Becher et al. 2013; Henry et al. 2017; Chen et al. 2021).

The BEEHAVE model (Becher et al. 2014) considers both within-hive and environmental factors. It has been used in over 25 studies to investigate topics such as the risk of colony mortality due to hornet predation (Requier et al. 2019; Requier et al. 2023), the effect of crop diversity and field structure (Horn et al. 2021), and the prediction of colony responses to pesticides (Rumkee et al. 2015; Prado et al. 2019). However, BEEHAVE uses a fixed bell-shaped curve to describe the queen bee's egg-laying rate throughout the year. The timing of the start, maximum, and end of egg laying is fixed and determines the yearly demography of the entire colony. In reality, the queen bee's egg-laying rate is affected by various external and internal conditions, including seasonal, nutritional, and social factors (Fine et al. 2018). Restricting the egg-laying rate to a bell-shaped curve limits BEEHAVE's application to Central European regions, as this curve is based on Central European data (Bodenheimer 1937; Schmickl and Crailsheim 2007).

In other parts of the world, egg laying may start sooner or later, and the season may be longer or shorter, depending on local weather conditions and pollen availability. Similarly, climate change can advance the onset of flowering (Templ et al. 2017), leading to earlier foraging periods. Favourable weather and forage conditions may advance egg laying, as the initial brood rearing following winter seems to be triggered by increasing temperatures (Nürnberger et al. 2018), thereby altering colony demography – a scenario that BEEHAVE is currently unable to simulate. This restricts the usefulness of BEEHAVE outside Central Europe and in changing climatic conditions, particularly with regard to predicting *Varroa* mite dynamics, as earlier egg laying means that the mites, which reproduce in capped brood cells, can cause more damage as their exponential growth begins earlier (Frey et al. 2013).

Several assumptions about how external and internal factors might trigger egg laying were implemented and tested to determine whether these assumptions could lead to realistic colony dynamics, e.g. growth in spring, a peak in early summer, and a decline after the peak. It was assumed that the queen responds rapidly to changes in pollen availability. A feedback loop was also considered, in which brood size affects pollen intake through the production of brood pheromones that encourage workers to forage for pollen resources (Eckert et al. 1994).

This study is intended as a heuristic because the empirical basis of the tested assumptions remains incomplete. Furthermore, even the best-performing version of the model produces unrealistic results for longer forage gaps. However, as Grimm and Berger (2016) noted, more is often learned from the limitations of models than from their calibrated 'good' behaviour. This work is intended to stimulate new empirical and theoretical studies that shed more light on the factors that trigger the queen's egg-laying behaviour. BEEHAVE-PPE should therefore be viewed as an exploratory extension of BEEHAVE rather than as a replacement for the original model.

The original BEEHAVE model

BEEHAVE, developed by Becher et al. (2014), is a model of a single honey bee colony that links internal processes with resource availability and weather conditions in the surrounding landscape. To date, it has been used in over 25 applications (Suppl. material 1: supplement S1.1). The "BEEHAVE for BeeMapp" version was used, which was run using NetLogo 6.2 (Wilensky 1999) after some syntactic updates were made (Suppl. material 1: supplement S2).

BEEHAVE comprises three modules: the colony module, the mite module, and the foraging module. BEEHAVE's external drivers include weather, represented by input files detailing daily foraging hours, and the daily availability of nectar and pollen on different flowering patches in the surrounding agricultural landscape. In the standard settings of BEEHAVE, the provision of forage in the landscape is summarised into two stylised flower patches, referred to as the 'Red' and 'Green' flower patches. These patches are located at different distances from the hive and focus on early and late flowering plants, respectively.

BEEHAVE-PPE including the new egg-laying module

A full overview and explanation of the modified model are provided in a model description following the ODD (Overview, Design concepts, Details) protocol (Grimm 2020; Grimm et al. 2006; Suppl. material 1: supplement S2). The corresponding NetLogo code, as well as the master's thesis on which this work is based, is available in a GitHub repository[1]. Fig. 1 provides an overview of the relationship between pollen and egg-laying in BEEHAVE and the new version, BEEHAVE-PPE. The mechanisms that were introduced are described below.

Egg-laying driven by the availability of pollen

For BEEHAVE-PPE, it was assumed that egg-laying is first affected by the amount of stored pollen available on a given day (see Fig. 1). The egg-laying rate ELR(d) on a certain day d is the product of the amount of pollen stored, PollenStore_g(d), and the new parameter EggsPerPollen_g, which defines the number of eggs that can be produced per gram of stored pollen. A linear relationship between stored pollen and egg laying was assumed as the simplest biologically plausible approximation, reflecting that the queen's egg production depends on nutrient intake from consumed pollen. If ELR(d) is larger than the maximum number of eggs the queen can lay in one day, defined by the parameter MAX_EGG_LAYING, ELR(d) is reduced to MAX_EGG_LAYING. In addition, it was assumed that the number of eggs laid per day changes only gradually, as some physiological inertia in egg-laying is assumed (Fine et al. 2018; Aamidor et al. 2022). Therefore, the possible daily change in ELR(d) was limited by averaging the newly calculated value with the average of the previous nine days. As empirical data to parameterise the exact adjustment speed of egg laying are not available, a 10-day moving average was used as a pragmatic approximation, consistent with the BEEHAVE assumption of approximately 7-day pollen reserves and extended slightly to account for sustained weather effects and physiological inertia.

1 https://github.com/Lamdom97/Masterarbeit-BEEHAVE.

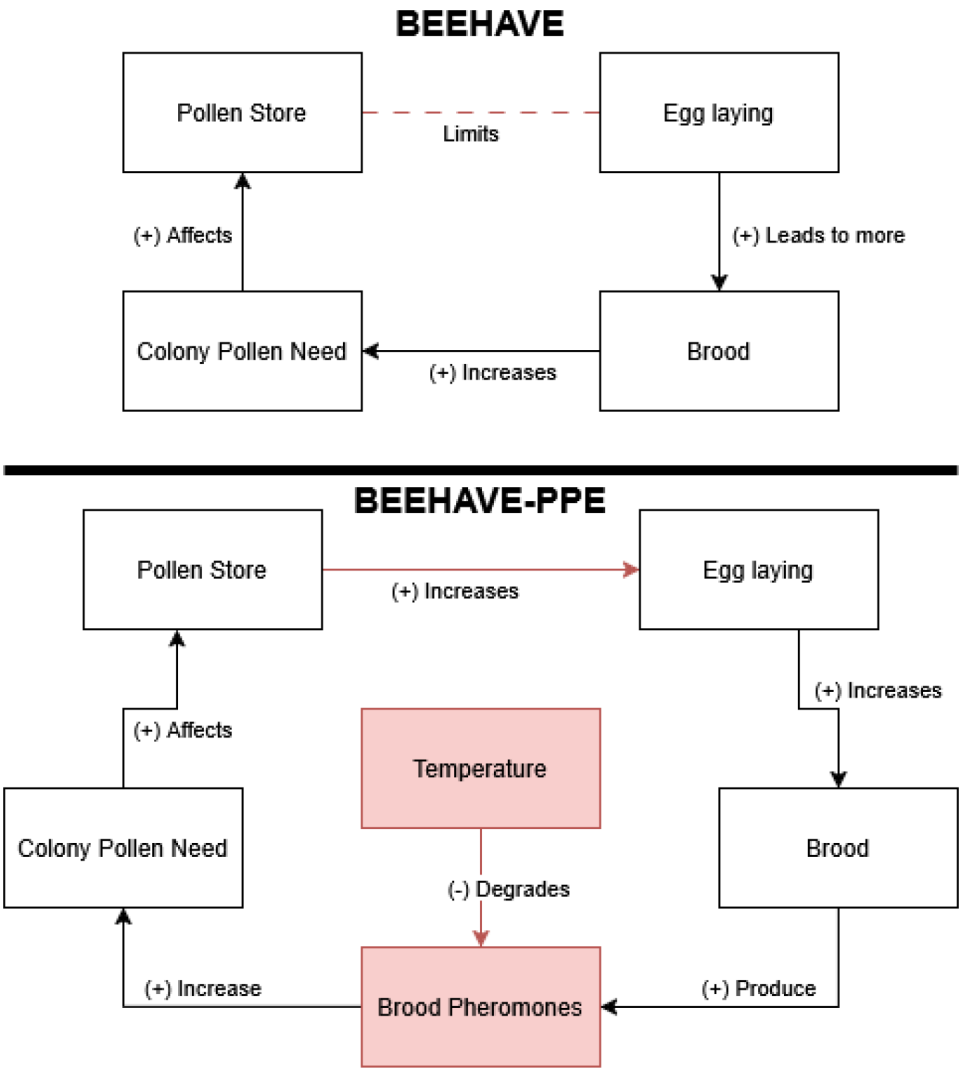

Figure 1. Conceptual overview of the relationships between stored pollen and egg-laying in BEEHAVE and the new version, BEEHAVE-PPE. Major differences are indicated in red. This includes the use of temperature, the presence of brood pheromones, and the connection between pollen stores and egg laying. In BEEHAVE, egg-laying leads to an increasing pollen store, but the pollen store only has an indirect effect on egg-laying by limiting, not increasing, egg laying. In BEEHAVE-PPE, egg-laying and pollen stores create a feedback loop, which is moderated by external temperature.

Pollen foraging affected by brood pheromones

Another factor that might affect the amount of pollen collected and stored was considered: brood pheromones. Bee larvae produce these pheromones, which affect the behaviour and development of bees in several ways (Pankiw 2004, 2007). An increase in brood pheromones generally leads to more pollen being collected and stored, with increased pollen loads per foraging trip and shorter resting periods between flights for individual bees (Pankiw 2004, 2007).

These effects were summarised by focussing on the proportion of foragers that collect pollen instead of nectar, i.e. BEEHAVE's original variable parameter ProbPollenCollection. The newly introduced terms represent the effect of brood pheromones on ProbPollenCollection, whereas the remaining terms remain unchanged from the original BEEHAVE formulation. For clarity, the newly introduced terms are shown in bold in the following equation. It was assumed:

$$\mathrm{ProbPollenCollection} = (1 - \mathrm{PollenStore_g}/\mathrm{IdealPollenStore_g}) * \quad (1)$$

$$\mathrm{MAX_PROPORTION_POLLEN_FORAGERS} *$$

$$\mathbf{influenceLim} * (\mathbf{1} - \mathbf{1}/\mathbf{exp}(\mathbf{concScale} * \mathbf{BP_ratio}))$$

Each simulation day, before the start of the foraging module, each larva produces 0.1 units of brood pheromone. The total amount of brood pheromone in the colony is then stored as the dimensionless variable BroodPheromone, which enters Eq. 1 via BP_ratio, defined as BroodPheromone divided by the number of adult bees.

In the original BEEHAVE model, ProbPollenCollection is determined by the ratio of currently stored to ideal pollen reserves, where ideal reserves are defined as daily pollen consumption multiplied by 7. It is capped by MAX_PROPORTION_POLLEN_FORAGERS at 80% to ensure that at least 20% of foragers collect nectar. In BEEHAVE-PPE, the new parameters influenceLim and concScale in Eq. 1 quantify the additional brood-pheromone effect on this baseline relationship: influenceLim determines the maximum magnitude of the new term, while concScale determines how rapidly bees respond to increasing brood pheromone concentrations.

As influenceLim and concScale are fixed parameters, only BP_ratio varies over time. The brood-pheromone term in Eq. 1 increases asymptotically from 0 to influenceLim with increasing BP_ratio. For a given value of BroodPheromone, adding bees reduces the incentive to collect pollen, whereas removing bees increases it. This assumption creates a relationship between the number of larvae producing brood pheromone and the number of adult bees in the hive: to achieve the same effect on ProbPollenCollection in a large colony, more larvae are needed than in a small colony. This assumption is supported by the observation that foragers can encounter brood pheromones via communal feeding by nurses that have recently fed larvae. It is further supported by the observation that the degradation rate of brood pheromone components is several orders of magnitude lower than that of other bee pheromones (Ma et al. 2018). Consequently, brood pheromone signals were detected throughout a honey bee colony, suggesting colony-wide effects on workers performing different activities (Johnson et al. 2010).

In spring, the ratio of brood pheromone to adult bees is high because brood is abundant while the number of newly emerged adult bees is still relatively low. This high BP_ratio increases ProbPollenCollection, which promotes pollen collection and supports egg laying and brood production through improved pollen availability. In summer, BP_ratio declines as the adult population increases relative to brood, while higher temperatures further reduce it by accelerating brood pheromone degradation. This shifts foraging effort more strongly towards nectar collection, lowering pollen availability and thereby reducing support for brood production. Later in the year, lower temperatures slow degradation and can increase BP_ratio again, causing a modest shift back towards pollen collection and a corresponding small recovery in population growth.

In real colonies, winter bees differ physiologically from summer bees and survive over winter. They serve as living nutrient storage and contribute to initiating the first brood cycle (Knoll et al. 2020) and likely early pollen foraging. Because BEEHAVE does not explicitly represent separate winter and summer

Table 1. Six new parameters of BEEHAVE-PPE (Suppl. material 1: supplement S2.7.2.).

Description	Parameter	Value
Upper limit of brood pheromone influence	influenceLim [-]	2.35
Scaling of brood pheromone concentration	concScale [-]	0.3
Eggs laid per gram of pollen	EggsPerPollen_g [Eggs/g Pollen]	18
Reference temperature (Arrhenius equation)	T_ref [°C]	27°
Reference reaction rate (Arrhenius equation)	k_ref [1/day]	0.44
Activation energy (Arrhenius equation)	E_a [kJ/mol]	147

worker types, this distinction is implemented here as a structural approximation in the BP_ratio calculation. Specifically, only bees hatched in the current simulation year are counted for BP_ratio, whereas bees hatched in the previous year are treated as winter bees. This treatment captures the early-season role of winter bees while avoiding excessive dilution of the brood-pheromone signal, which would otherwise prevent initiation of the brood-pheromone-driven pollen-foraging feedback. As a consequence, BP_ratio can be high early in the simulation year, which in the model increases the incentive for pollen foraging; given limited empirical information on overwintering-to-spring transition dynamics, this should be interpreted as a pragmatic structural approximation.

In addition, the influence of ambient temperature on brood pheromone degradation was implemented using the Arrhenius equation, introducing three additional parameters (Table 1, Suppl. material 1: supplement S1.3, S2). The assumption that ambient temperature affects pheromone degradation within the hive might appear unrealistic, since honey bees regulate in-hive temperature. However, outside temperature affects active foragers, and temperature still varies outside the brood area (F. Pohl pers. communication).

Simulation settings and calibration

Monitoring data from France involving 250 colonies were used to prepare the weather input files and to calibrate and test BEEHAVE-PPE (Suppl. material 1: supplement S1.9). The new egg-laying module introduces six parameters (Table 1), which were calibrated using the NetLogo tool BehaviorSearch (Stonedahl and Wilensky 2010; Suppl. material 1: supplement S1.6). Because empirical data were only available from March to October, a continuous reference curve covering the full year was derived from the empirical data using cubic-spline interpolation and used as the calibration target. Parameter sensitivity was assessed using local one-at-a-time analysis and global sensitivity analyses based on the Morris and Sobol methods (Suppl. material 1: supplement S4.2, S4.3).

Simulations were run using the default BEEHAVE landscape, consisting of two flower patches at different distances from the hive (Fig. 2), which was treated as a high-resource environment without intended seasonal floral limitation. The parameters determining the onset of resource availability are SHIFT_G and SHIFT_R. SHIFT_G was set to -80 instead of the standard -40, while SHIFT_R was left at its default value of 30 to maintain high floral resource availability throughout the simulated foraging season (February–November), rather than to match a specific regional flowering calendar.

Simulations were also run in which both flower patches provided maximum nectar and pollen throughout the year. This allowed testing of whether the origi-

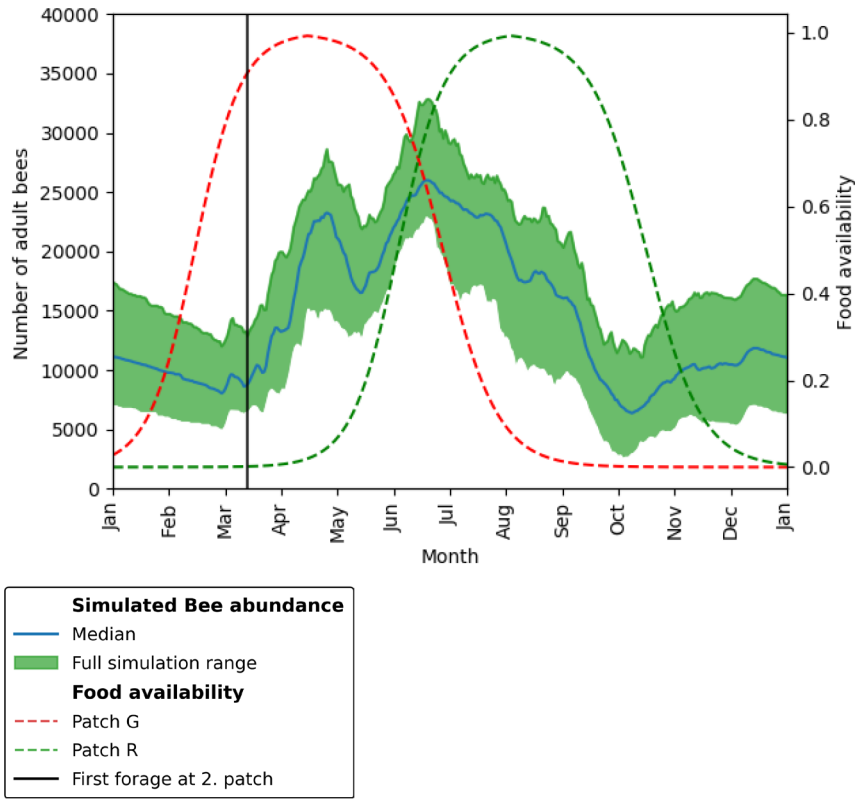

Figure 2. Full simulation range, from the minimum to the maximum of all simulations (green shaded area), and the median adult bee population size (blue line) using BEEHAVE-PPE in the third year of simulation, 200 simulations, as well as the food availability for both flower patches (dashed red and green lines). The vertical black line shows the first day (day 73) on which foraging at the second, green flower patch is possible. Parameters: Suppl. material 1: supplement S1.8.

nal scenario of two overlapping bell-shaped resource curves produced artefacts with the new egg-laying module (Suppl. material 1: supplement S1.7) and isolation of the effects of temperature and foraging hours on colony development.

For all simulations, the mite module and beekeeper actions were disabled, and the colony was initialised with 10,000 bees on 1 January. For each simulation, 200 replicates were run over 3 years, and only results from the third year were analysed. The queen's maximum egg-laying rate was set to 1,600 eggs per day, consistent with the default value in the original BEEHAVE model. To assess the influence of this fixed setting, the simulations were repeated while varying the maximum egg-laying rate by multiplicative factors ranging from 0 to 2 under otherwise identical settings (Suppl. material 1: supplement S4.1).

Results

Pollen-driven egg-laying by itself was not sufficient to produce realistic seasonal egg-laying and colony development (Suppl. material 1: supplement S1.3, fig. S1, green curve). Using the full BEEHAVE-PPE model, colony development showed three peaks during the simulation year: in April, in June, and in December (Fig. 2). After the second peak, the number of adult bees began to drop until the end of the foraging season in October, as existing brood continued to develop into adult bees while the production of additional brood

slowed down. The two population peaks in April and June are linked to a temporary increase in unsuccessful (empty) foraging flights in the shifted two-patch setup. This reflects a setup-specific artefact of the foraging module: after the green patch becomes available, foragers increasingly search there for pollen, even when the patch does not provide enough pollen for consistently successful collection, leading to more empty flights and temporarily reducing effective pollen intake. A similar pattern can be reproduced in the original BEEHAVE when patch timing is shifted, e.g. via SHIFT_G, but its demographic effect is comparatively limited there (Suppl. material 1: supplement S1.7); in BEEHAVE-PPE, reduced pollen intake has stronger downstream effects because it feeds back directly on egg laying and brood production.

Assuming constantly high resource availability year-round at both flower patches, the drop in adult numbers in May was mostly absent, while the peak in December was not affected (Fig. 3). Compared with the default scenario (Fig. 2), median colony size continued growing until a single population peak was reached in June. The population peak was higher than in Fig. 2, reaching approximately 34,000 adult bees rather than 25,000. After the peak, the population dropped faster than before and reached a similar number of adult bees in October compared with the default patch scenario (Fig. 2).

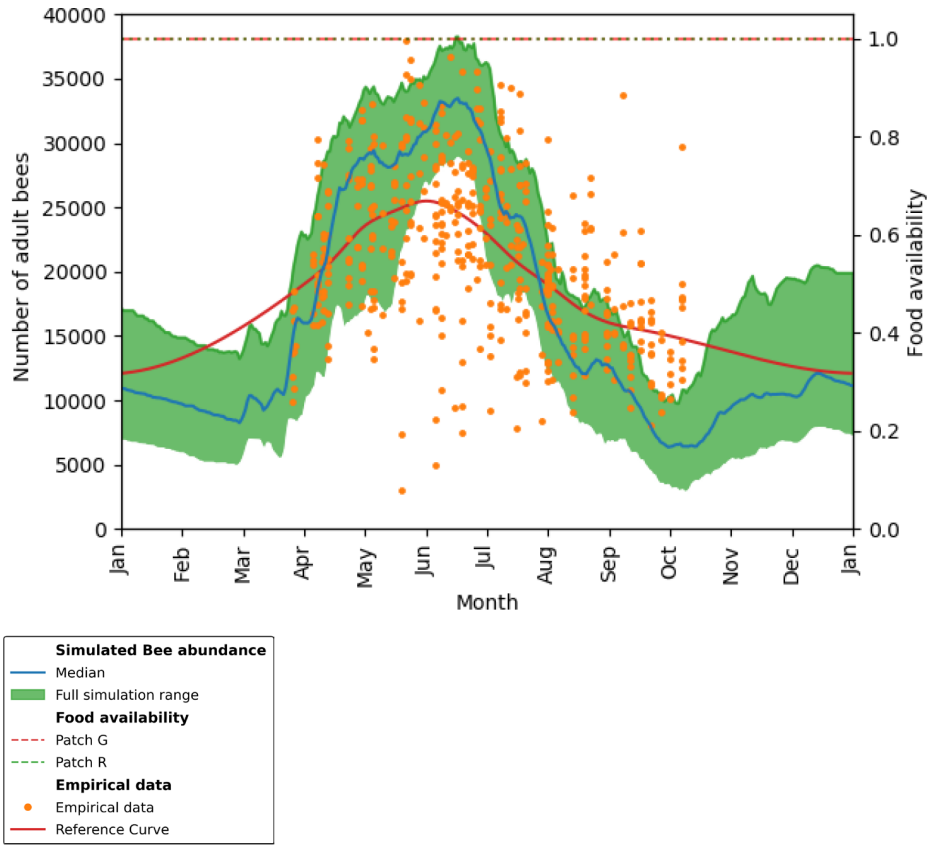

Figure 3. Full simulation range, from the minimum to the maximum of all simulations (shaded green area); and median adult bee population (blue line) using BEEHAVE-PPE, 200 simulations, in the third year of simulation; mean population values of the French dataset (orange points); and interpolated reference curve (red line). The available amount of pollen and nectar per day was constant, i.e. 1 kg and 20 L, respectively, for the whole year. Parameters: see Suppl. material 1: table S1.2.

For constant maximal pollen and nectar availability, egg-laying and colony development are fully determined by temperature, foraging hours, and the resulting egg-laying rate. The resulting timing of the colony peak and decline is consistent with the empirical data (Fig. 3). The first sustained foraging period begins in February (Fig. 4), followed by increasing egg production and a delayed increase in adult population size. Egg production reaches high values early in the season and remains high through spring, resulting in colony growth towards the summer peak. The subsequent decline starts while foraging hours are still near their seasonal maximum in July, indicating that reduced foraging time is not the primary driver of the population decrease. Instead, persistently high summer temperatures from July to September reduce egg-laying, followed by a decline in colony size. As temperatures decrease again towards autumn, this temperature-driven pressure is relaxed, allowing renewed egg-laying and a smaller late-season rise in colony size.

Varying the fixed maximum egg-laying rate mainly affected the overall colony size, whereas the general shape of the population trajectory and the timing of seasonal population peaks remained largely unchanged across moderate parameter changes; only more extreme values altered these dynamics more strongly and reduced colony stability (Suppl. material 1: supplement S4.1). Local and global sensitivity analyses showed that colony outcomes were most strongly influenced by the temperature- and pheromone-related parameters. In the local analysis, the

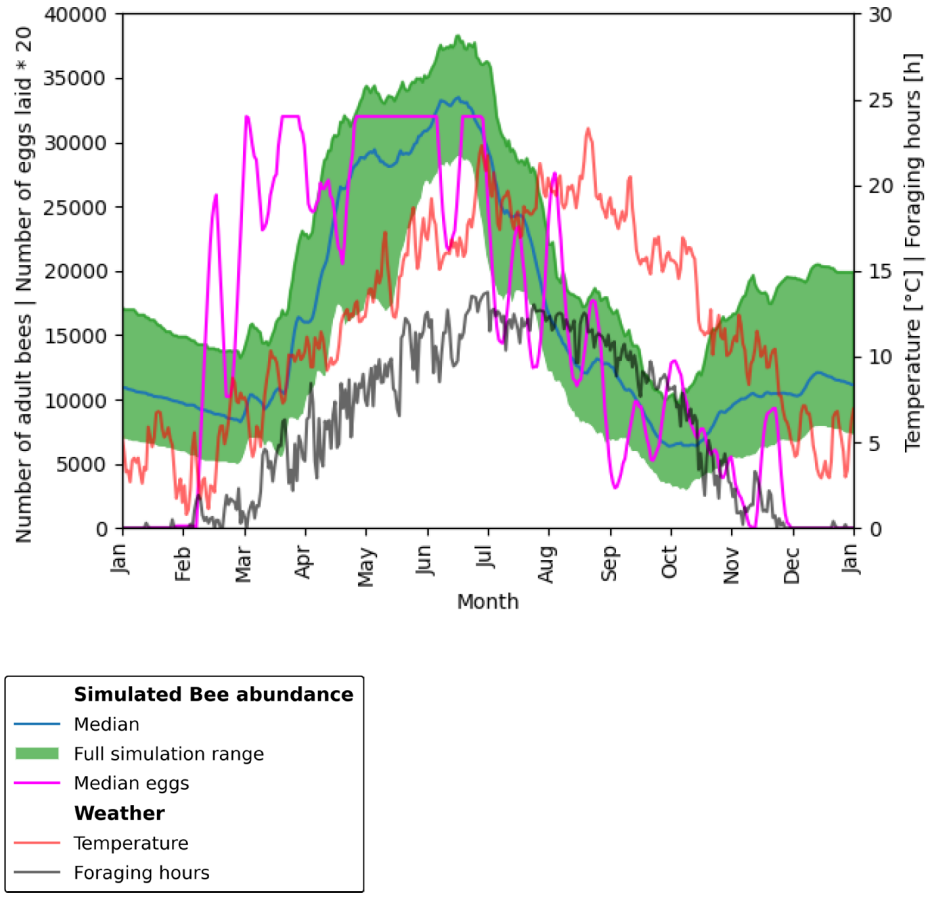

Figure 4. Simulation as in Fig. 3, but temperature (red), foraging hours (black), and daily egg-laying rates (magenta) are also shown. Temperature and foraging hours share the right axis, as both values do not exceed 24 °C or 24 h. Parameters: see Suppl. material 1: table S1.2.

Arrhenius reference temperature (T_ref) was the most sensitive parameter, indicating that model behaviour is strongly affected by thermal conditions around the calibrated temperature range, with higher or lower peak temperatures possibly causing larger deviations in the population trajectory. In the global analyses, activation energy (E_a; Arrhenius temperature-sensitivity term) and concScale were the dominant drivers overall, with T_ref and the Arrhenius reference reaction rate (k_ref) as secondary contributors and stronger interaction effects for survival-related metrics (Suppl. material 1: supplement S4.2, S4.3). These results imply that applying BEEHAVE-PPE to other climates or years requires careful local calibration of temperature-response and brood-pheromone-response parameters.

Discussion

With the new BEEHAVE-PPE module, a new positive feedback loop is introduced: once the first larvae hatch and produce brood pheromone, positive feedback is initiated, causing more pollen to be collected and more eggs to be laid. This continues until higher temperatures lead to faster degradation of brood pheromone and, therefore, reduced pollen collection. A population peak follows, which emerges in summer when temperatures are at their maximum. Even though foraging hours are maximal in this period, temperature has a stronger effect, and foragers shift from pollen to nectar collection, which reduces reproduction and leads to declining colony size. This timing is consistent with both the empirical colony observations and the interpolated reference curve (Fig. 3), which show a summer population peak followed by decline despite favourable foraging duration. This modelled shift in foraging focus is biologically plausible but remains a hypothesis requiring direct empirical confirmation.

With BEEHAVE-PPE, temporary reductions in pollen intake can weaken the brood-pheromone-reproduction feedback without fully collapsing it. In Fig. 2, this is visible during the period affected by the increased number of unsuccessful foraging flights: reduced effective pollen intake temporarily dampens brood production, leading to population decline, but the feedback loop remains active, allowing recovery towards the second peak and eventual colony survival. In contrast, repeated or prolonged disruptions, e.g. persistent bad-weather periods, can drive the system into a low-pollen, low-brood, low-pheromone state, where reduced pollen intake lowers egg laying, fewer larvae produce less brood pheromone, and the weakened pheromone signal further suppresses pollen collection. This decline can lead to colony mortality in BEEHAVE-PPE. This indicates that, in its current form, BEEHAVE-PPE has limited buffering capacity against short-term pollen deficits, such that temporary disruptions can lead to feedback collapse under repeated stress. In the original BEEHAVE, this failure mode is weaker because egg laying is imposed and not directly coupled to short-term pollen limitation.

In general, all assumptions about the processes that govern the production and disappearance of brood pheromones in the BEEHAVE modification are experimental and not yet fully supported by empirical evidence. Nevertheless, in reality, the queen bee's egg-laying rate is unlikely to be independent of weather and colony structure, as assumed in BEEHAVE. It is known to be strongly affected by the pollen fed to the queen (Fine et al. 2018) and, therefore, by in-hive pollen availability, which depends not only on the level of pollen foraging but also on pollen availability in the landscape.

Moreover, brood demand for pollen feeding may be signalled within the hive via brood pheromones. Forager bees may increase pollen foraging effort by increasing the size of collected pollen loads and decreasing resting time between forage flights (Pankiw 2004). This change in behaviour can be reinforced or diminished by artificially increasing the amount of brood pheromone or restricting the available brood area (Rotjan et al. 2002; Weidenmüller and Tautz 2002).

However, research on brood pheromone effects is still sparse, and brood pheromone dynamics have not previously been modelled as a direct driver of colony population dynamics. Consequently, several simplifying assumptions were required. In particular, temperature-dependent brood pheromone degradation was necessary to reproduce realistic seasonal dynamics, whereas temperature-independent degradation did not reproduce the summer downturn in egg-laying and the subsequent population decline (Suppl. material 1: supplement S1.3). As shown in Fig. 4, under temperature-dependent degradation, persistently high summer temperatures reduce egg laying and subsequently lead to declining simulated colony size, even while foraging duration remains high. The resulting seasonal timing is plausible, as simulated peak-and-decline timing matches the empirical data (Fig. 3), but broader multi-year datasets linking temperature and colony demography are needed to test this mechanism more directly.

BEEHAVE-PPE appears highly sensitive to weather input. For parameterisation and simulations, weather averaged across multiple years was therefore used to reduce repeated disruptions in pollen intake, i.e. periods with strongly reduced or effectively zero foraging, typically during unfavourable weather. In BEEHAVE-PPE, repeated disruptions can trigger collapse of the pollen-brood-pheromone feedback loop: reduced pollen intake lowers egg laying, fewer larvae produce less brood pheromone, and weakened brood-pheromone signalling further reduces pollen-focused foraging. Thus, collapse is driven by both constrained resource intake and reduced reproduction. Smaller disruptions can already be handled, as shown in Fig. 2, where a prolonged decline in effective pollen intake weakens the feedback and causes temporary population decline but does not fully collapse the cycle and is followed by recovery. It may be possible to buffer stronger disruptions using mechanisms that are already present in BEEHAVE, especially brood cannibalism and nurse-bee self-metabolisation. However, substantial adaptation would be required. First, brood cohorts would need explicit nutritional state variables so that cannibalism can reclaim and redistribute nutrients, instead of the current brood removal without resource reclamation. Second, nurse cohorts would need explicit internal nutrient reserves that are dynamically depleted and replenished according to pollen availability and brood-feeding demand, instead of the current single-factor approximation. Implementing this would also require explicit alignment with pollen nutritional value, especially protein content, and broader model-wide rebalancing so these nutritional flows are represented consistently across colony processes.

Although the main reason for developing BEEHAVE-PPE was to replace the imposed egg-laying function, the maximum number of eggs laid per day was kept unchanged. Attempting to remove this limit led to generally worse model fits to the data during parameterisation, as early population growth became excessively fast. The maximum number of eggs a queen can produce is an emergent property of multiple factors that are only partially understood at present. In general, modelling properties as emergent rather than imposing hard limits is

preferable, but this requires sufficient information to understand the underlying rules, which was not the case here. Therefore, keeping the maximum number of eggs unchanged for this study helped to prevent the introduction of further assumptions. Further development of BEEHAVE-PPE will likely involve removing this artificial limit, but this will require more research into egg-laying.

Conclusion

In conclusion, the new egg-laying module provides a mechanistic alternative to the imposed egg-laying curve in the original BEEHAVE model. By linking pollen intake, brood pheromone signalling, and egg laying, BEEHAVE-PPE reproduces plausible seasonal colony dynamics driven by external conditions. At the same time, the model highlights the need for stronger empirical evidence on the factors controlling queen egg laying and on how brood pheromone shapes colony-level responses. In particular, future work should focus on direct measurements of how pollen availability, brood pheromone signalling, and temperature jointly influence egg-laying dynamics and seasonal colony development. Such data would not only improve model calibration but also allow the relationship between temperature and typical seasonal population trajectories to be tested more directly, thereby strengthening the model's predictive value.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
No AI tools were used in the preparation of this manuscript.

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Author contributions

Conceptualization: DL, AF, JG. Data curation: DL, FR, JG. Formal analysis: DL. Investigation: DL, FR, AF, JG. Methodology: DL, AF, JG, FR. Resources: FR, AF, JG. Software: DL. Supervision: AF, JG Visualization: DL. Writing - original draft: DL. Writing - review and editing: DL, FR, AF, JG.

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Data availability

All data generated and analyzed during the present study are included in either the article itself or the Supporting Information. The full model code is available as a GitHub repository at: https://github.com/Lamdom97/Masterarbeit-BEEHAVE.

Supplementary material 1

Supplementary information

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Data type: docx
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