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A computational analysis of honeybee colony collapse prediction model and simulations

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ABSTRACT

Honeybees play a critical role as natural pollinator and are essential to global food production. Monitoring honeybee population densities can provide valuable insights into the environmental status of a given region, although effectively carrying out such monitoring is challenging. To address this issue, this study focused on the development of a mathematical model to predict population density and detect potential colony collapse. The model utilized a set of effective arrays of differential equations that consider crucial parameters. Analyzing actual data using the model revealed that regions with higher flower densities experienced reduced vulnerability to unnatural deaths or diseases, while those with lower flower densities tended to have smaller populations. Furthermore, numerical simulations showed that unnatural death rates exerted the most significant impact on the model. In adverse environmental conditions, forager populations decline first, leading to decreased food availability and potential colony collapse. This model, as a highly practical tool, holds immense value for environmentalists seeking precise predictions of honeybee population density within their respective regions.

Keywords: honeybee population; honey storage; honeybee colony size; colony collapse; multi–stage model

1. INTRODUCTION

As the world becomes more densely populated, food shortages have become a critical issue for humanity. Plants and trees serve as major sources of food for humans and animals, providing grains, seeds, and fruits. Moreover, previous research has discovered that over three-quarters of all flowering plants, which constitute a significant part of the human diet, depend on animal pollination (Klatt et al., 2014; Feldman, 2006). Bees are among the most common pollinators, spending most of their time accumulating pollen and nectar. The short hair on their bodies facilitates pollen adherence, ensuring easy transfer of pollen.

Despite the benefits honeybees bring to the ecosystem, their population densities have been unstable over the past fifty years, depending on environmental condition of their habitats. Globally, research indicated that since 1973, honeybee colony densities in Asia have increased nearly 3-fold, while in North America, they have decreased to around 43% of the initial level (Jacobson et al., 2018).

Monitoring the population density of honeybees presents a practical challenge, as it cannot be determined simply by counting the number of bees. Instead, it is assessed by measuring the weight of the hive itself, requiring special expertise and expensive equipment (Fitzgerald et al., 2015). Another complicating factor is that the measured hive weight includes not only bees but also honey and wax. This makes it difficult to directly correlate weight with population, especially during rapid declines, as the weight of wax does not decrease at the same rate. Moreover, using scales in harsh or remote environments is often unfeasible and, under harsh environmental conditions, it can lead to erroneous results.

Computational analysis is emerging as a superior alternative for acquiring and predicting honeybee population size, as it can simplify data collection and be more cost-effective. Such analyses typically rely on initial conditions within the hive, such as the queen's egg-laying rate, which is time-dependent and influenced by seasonal variations (Messan et al., 2021; Kang et al., 2016). The duration of each stage in the honeybee life cycle has also been investigated, with drones spending approximately 24 days in the brood stage and workers spending around 21 days (Chen, 2020).

Existing honeybee population prediction models often employ a multi-stage approach, dividing the honeybee life cycle into stages such as brood and adult (Chen et al., 2020). Some models have utilized recruitment rates, referring to the rate of development from one stage to the next (Dennis and Kemp, 2016). Other multi-stage models incorporate worker sub-stages and consider food storage within the hive (Perry et al., 2015). However, these models primarily serve as frameworks and are not specifically designed for predicting colony collapse under real-world conditions.

Therefore, this report introduced a honeybee population model that has been developed, encompassing a broader spectrum of life stages than existing models. Our model considered multiple bee life cycle stages, fluctuating queen egg-laying rates, seasonal variations, the weight of honey stored in the hive, forager activity rates, and population density, and was capable of predicting instances of potential colony collapse. Our model aimed to assist beekeepers and environmentalists in adapting their treatment plans for apiaries, ensuring integrity of the colony population while maximizing honey production.

2. MATERIALS AND METHODS

2.1 Materials

Numerical simulations were conducted using Python version 3.10.12 along with the following mathematical libraries (NumPy version 1.22.4, Pandas version 1.5.3, Matplotlib version 3.7.1, Scikit-learn version 1.2.2, and Seaborn version 0.12.2), operating on the MacOS Ventura operating system.

Values for the male brood/entire brood ratio, the time immature workers and drones spend in the brood stage, and the time foragers spend in the immature worker stage were obtained from Chen et al. (2020), Khoury et al. (2013), DeGrandi-Hoffman et al. (1989), and Page and Metcalf (1984). Otherwise, all other model inputs were estimated to fall within the habitable range.

2.2 Model formation

The life cycle of a honeybee consists of four distinct stages: egg, larva, pupa, and adult. In this context, we refer to the combination of egg, larva, and pupa as a brood. Additionally, adult honeybees were classified into different groups based on their roles. Females were divided into immature workers, and foragers, while males are drones.

After spending approximately 21 to 26 days within the hive as brood, the female pupae will be fully developed into immature workers and the male pupae will have developed into drones. The role of the honeybee depends on their age polytheism; a young worker spends their day cleaning the hive and nursing broods, while a forager spends their day harvesting pollen and nectar (Moore et al., 1987; Johnson, 2010). Therefore, natural and predatory death rates cannot be equal in each life cycle stage.

A previous model was constructed by dividing the bee life cycle into 2 stages: brood and adult (Chen et al., 2020). However, in our model, we aimed to improve accuracy by dividing the life cycle into 3 stages: brood, immature worker, and forager, due to the fact that each type of adult honeybee serves a different role in the dynamic of the colony population.

The construction of the model was based on the following assumptions. To introduce variability and enhance the realism of the number of eggs laid per day, a normally distributed egg-laying rate was assumed. Typically, a queen bee has an average lifespan of over 3 years, and in some cases, it may exceed 5 years. As the queen bee typically remains within the hive, rendering the risk of predation negligible, her lifespan can be set at the maximum level. Since drones have a significant impact on the colony's population, they are treated as a separate class from other groups, and their sole role is to mate with the queen, they remain inside the hive.

Environmental factors (climate and temperature, and season) can profoundly impact honeybee populations. The equation from Messan et al. (2021) was modified to define a seasonal factor (Ω_t) as shown in Equation (1):

$$\Omega_t = 1 + \vartheta \cos\left(\frac{2\pi(t-45)}{365} + \phi\right) \tag{1}$$

where t is the time since the simulation started, ϑ is the seasonal impact degree, ranging from –1 to 1, and ϕ is the seasonal phase constant. The seasonal phase constant is added in the cosine term to accommodate the initial phase of seasonality.

2.2.1 Egg-laying rate

The number of eggs laid daily by the queen bee is dependent on season. Previous research has indicated that as the queen ages, her egg production rate continuously decreases, a trend reflected in our model through exponential decay (Coffey, 2007; Di Pasquale and Jacobi, 1998; DeGrandi-Hoffman et al., 1989). Equation (2) describes the number of eggs laid per day (r_t) as follows:

$$r_t = r_0 e^{-d_r t} \Omega_t \tag{2}$$

where r_0 is the maximal mean eggs laid per day, and t is the time since the simulation started which resets to 0 every 5 years. This reset corresponds to the assumption of a 5-year queen bee lifespan.

2.2.2 Rate of survival

At each stage of development, whether transitioning from brood to drone or immature worker, or from immature worker to forager, only a specific portion of the population will survive. It is important to note that the survival rate of all honeybees within the colony is influenced by their workload intensity, which we refer to as the level of activity. The exact definition and further explanation of this concept will be provided in section 2.2.5.2. Hence, to model the rate of survival, we modified the equation structure based on the activity level equation presented by Kang et al. (2016). We define the rate of survival Ψ_t following Equation (3):

$$\Psi_t = \frac{[A_t]^2}{K+[A_t]^2\Upsilon_t} \tag{3}$$

where $[A_t]$ is the number of adult bees at time t, $\sqrt{K}$ is the colony size at which brood survival rate is half maximum, and Υ_t is the level of activity at time t. As the level of activity increases, the rate of survival decrease; conversely, as the population size increases the rate of survival increases.

2.2.3 Brood demographics and population dynamics

The ratio between male brood and entire brood is defined as the constant λ. In other words, the number of male broods and female broods corresponds to $\lambda[B]$ and $(1-\lambda)[B]$, respectively. The constant λ is generally found to be in the range of 10%–15%, but for the ease of calculations, in the case of our model, it is fixed at 10% (Chen et al., 2020; Page and Metcalf, 1984).

By using the egg-laying rate (Equation (2)), and the rate of survival (Equation (3)), the rate of change in brood population can be described by Equation (4):

$$\frac{d}{dt}[B_t] = r_t - \Psi_{t-\tau}[B_{t-\tau}] \tag{4}$$

where $[B_t]$ is the population of brood at time t, r_t is the egg-laying rate at time t, τ_D is the time a drone spends in the brood stage, τ_W is the time an immature worker spends in the brood stage, and $\Psi_{t-\tau}[B_{t-\tau}]$ is the number of broods that progress into adult bees. We assumed that the natural death rate of the brood is already incorporated into in the fluctuation of the egg-laying rate of the queen bee.

2.2.4 Drone population dynamics

Drones (male honeybees) only represent a small portion of the whole population of a colony, but they are vital for its survival. The life cycle of a male honeybee is shown in Figure 1 (a).

To visualize the whole drone population dynamic, the natural death rate d_D is considered along with time spent in the brood stage. The time spent as brood for drones is around 24 days, or $\tau_D = 24$ (Chen et al., 2020; Khoury et al., 2013; DeGrandi-Hoffman et al., 1989). Therefore, the rate of change in the drone population can be described by Equation (5):

$$\frac{d}{dt}[D_t] = \lambda\Psi_{t-\tau_D}[B_{t-\tau_D}] - d_D\Omega_t[D_t] \tag{5}$$

where $[D_t]$ is the population of drones at time t, τ_D is the time a drone spends in the brood stage, $[B_{t-\tau_D}]$ is the population of brood at time $t-\tau_D$, and d_D is the drone death rate. The positive term on the right-hand side of the differential equation, $\lambda\Psi_{t-\tau_D}[B_{t-\tau_D}]$, represents the number of newly developed drones factored with the survival rate of the brood at time $t-\tau_d$. The time stamp $t-\tau_d$ in the survival rate is used because the newly developed drones originate from male brood at time $t-\tau_d$.

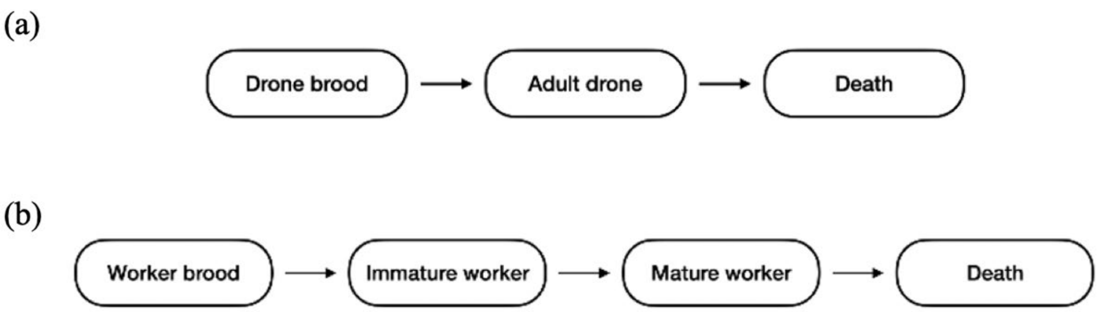

Figure 1. The life cycle of (a) male honeybee, and (b) female honeybee

2.2.5 Worker population dynamics

The honeybee population is primarily comprised of workers, and the number of workers in the colony has a ripple effect on the population dynamics of other honeybee segments. For example, the population of workers affects the survival rate of the brood, which directly impacts the population of drones. In this study, adult workers were further categorized into two sub-stages: immature workers and foragers. These sub-stages were interconnected, transitioning from worker brood to immature, from immature to foraging, and eventually finally to death. The life cycle of a worker is illustrated in Figure 1 (b).

2.2.5.1 Immature worker

The population dynamics of immature workers and drones are generally similar. Nevertheless, mortality resulting from the activity level has remained subtle given the less intensive role of the immature worker, compared to that of a forager. The population dynamics of immature workers are dependent upon the same rate of survival as the drone. The main difference is that as the immature worker ages, they tend to have a higher chance of surviving throughout the immature phase, and therefore the rate of survival of the immature worker can be modeled as the term $e^{-d_1\tau_W}$. The rate of change in the immature worker population is defined by Equation (6):

$$\frac{d}{dt}[W_{1,t}] = (1-\lambda)\Psi_{t-\tau_W}[B_{t-\tau_W}] - e^{-d_1\tau_F}\Psi_{t-\tau_W}[W_{1,t-\tau_W}] - d_1[W_{1,t}] \quad (6)$$

where $[W_{1,t}]$ is the population of immature workers at time t, τ_W is the time an immature worker spends in the brood stage, and τ_F is the time a forager spends in the immature worker stage. The first term on the right-hand side of the equation represents the number of broods that develop into immature workers at time t, the second term defines the number of immature workers that develop into foragers, and the third term corresponds to the death rate of immature workers.

2.2.5.2 Honey storage dynamics

The ability of a colony to store honey is another crucial factor dictating its survivability. Honey is made by collecting pollen and nectar from flowers outside the hive. Foragers are responsible for the duty of collecting ingredients for honey production, and for this reason, we define a level of activity coefficient that indicates how intensive the foragers are at harvesting. The higher the level of activity coefficient becomes, the more the foragers work. To construct this coefficient, the dynamics of honey storage need to be analyzed and translated. The rate of change in honey storage can be modeled by Equation (7):

$$\frac{d}{dt}[H_t] = \alpha\beta e^{-\frac{[W_{2,t}]}{\eta}}\Omega_t[W_{2,t}] - \gamma_A[A_t] - \gamma_B[B_t] \quad (7)$$

where $[H_t]$ is the amount of honey at time t, α is the honey production coefficient, β is the flower density, $[W_{2,t}]$ is the population of foragers at time t, η is the honey production efficiency, Ω_t is the seasonal flower blooming factor, $[A_t]$ is the population of adult honeybees at time t, $[B_t]$ is the population of broods at time t, γ_A is the consumption coefficient of an adult honeybee, and γ_B is the consumption coefficient of a brood. The exponential decay term on the right-hand side accounts for the interference created as the forager population grows.

Following the construction of the honey storage dynamics model, Equation (8) defines the level of activity of the forager:

$$\Upsilon_t = \frac{\tilde{H}\Omega_t}{[H_t]} \quad (8)$$

where Υ_t is the level of activity of the forager at time t, $\tilde{H}$ is the amount of honey at half maximum, Ω_t is the seasonal impact factor, and $[H_t]$ is the amount of honey at time t.

2.2.5.3 Forager population dynamics

Following on from the definition of honey storage in Equation (7) and the level of activity in Equation (8) the population dynamics of the forager is calculable by the Equation (9) below:

$$\frac{d}{dt}[W_{2,t}] = e^{-d_1\tau_F}\Psi_{t-\tau_F}[W_{1,t-\tau_F}] - \Upsilon_t[W_{2,t}] \quad (9)$$

where $[W_{2,t}]$ is the population of the foragers at time t.

Overall, the mechanism of the forager population dynamics is akin to that of the drones except for the death rate, which relies on the level of activity.

3. RESULTS

3.1 Simulation results

Since different landscape settings have their unique environmental parameter values, this section summarizes results of the numerical simulations with estimated parameter values to highlight the capabilities of the model.

3.1.1 Population dynamics

The following results arose from numerical simulations using our model, with inputs from a habitable environment. The results showed a periodic fluctuation when the system reached equilibrium, as illustrated in Figure 2, depicting the impact of seasonality on colony population. Additionally, Figure 3 (left) shows the rate of honey production over time, while Figure 3 (right) demonstrates that the model is sustained under an optimal conditional value, as the correlations do not converge.

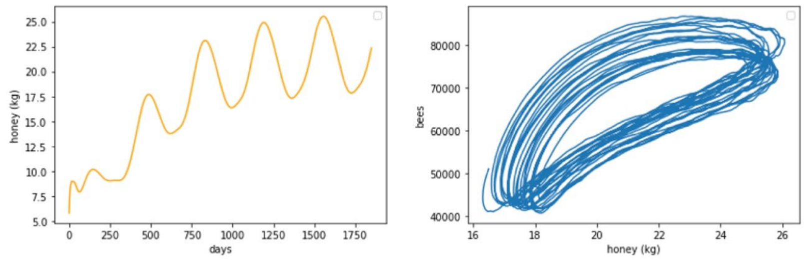

Figure 2. Graphs illustrating the dynamics of the honeybee population by segment (left) and the adult honeybee population (right)

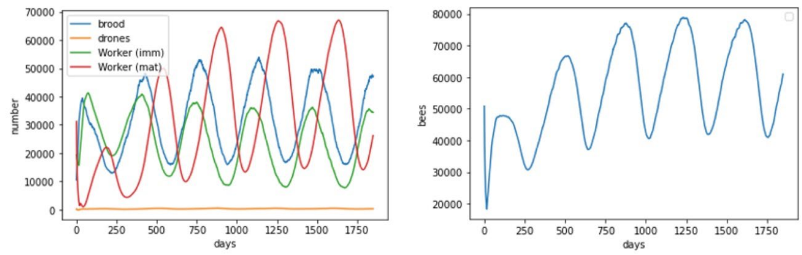

Figure 3. Graphs illustrating the amount of honey over time (left) and the correlations between the number of adult honeybees and the amount of honey (right)

Next, we simulated a scenario where the initial conditions are unhabitable for honeybees, to demonstrate colony collapse. The death rate was increased from day 1,000 until day 1,300. The results are illustrated in a 3–dimensional graph, depicting the relationship between the time interval, death rate, and honeybee population in Figure 4 (left). Additionally, Figure 4 (right) shows the correlation between the time interval, death rate, and the amount of honey (y–axis).

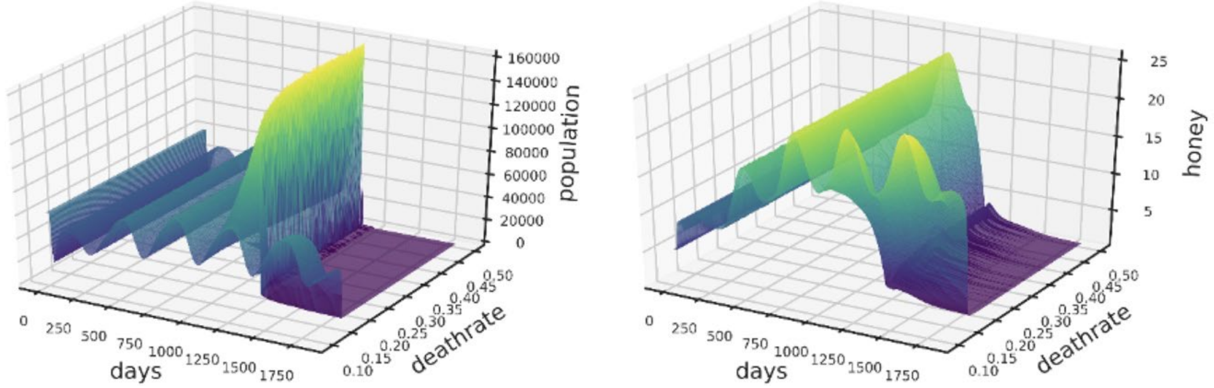

Figure 4. Graphs depicting the honeybee population dynamics (left) and the honey storage dynamics (right) with an increased death rate from day 1,000 until day 1,300, both illustrating the collapse of the honeybee colony

3.1.2 Colony collapse prediction

Given that natural conditions could not be replicated consistently, our model was designed to determine the relevant parameter thresholds, leading to the collapse of a bee colony. Consequently, the model can be applied by beekeepers to ensure the survival of their colonies. To apply the model effectively, variables crucial to bee population dynamics, such as flower density, death rate, and the maximal mean eggs laid per day, must be taken into consideration. Subsequently, we simulated our population dynamics model by varying these significant variables. The overall mechanism of the honeybee population dynamics model is shown in Figure 5.

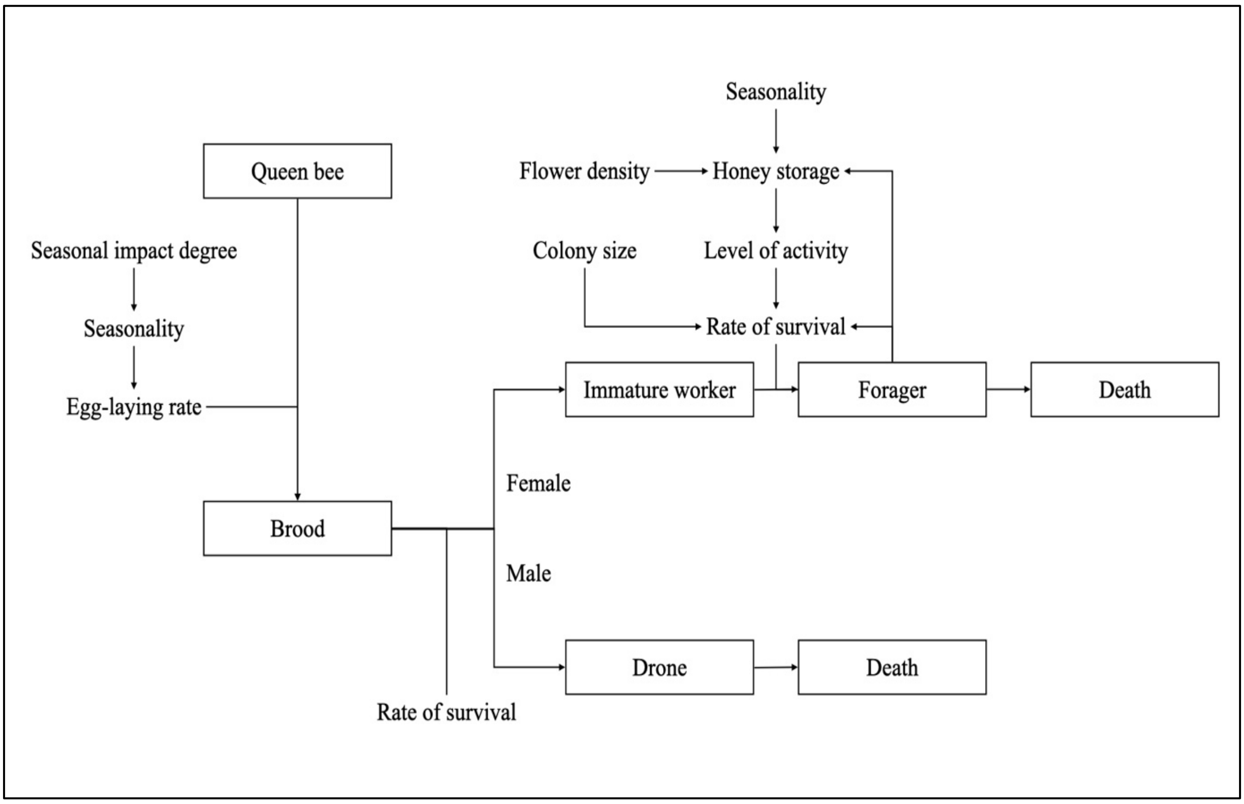

Figure 5. Diagram illustrating the impact of each parameter on the mechanism of honeybee population dynamics

3.1.2.1 Flower density cut-off threshold

Flower density is one of the most important environmental parameters in our population dynamics model, as it directly affects the forager population. Therefore, population dynamics were simulated to examine the impact of varying flower densities. The results of these simulations are shown in Figures 6(a) and (b). Notably, the simulations revealed that the honeybee colony could only be sustained when the flower density in the area was not lower than 1,420 flowers per square meter, based on our parameter settings.

3.1.2.2 Birth and death rates cut-off threshold

Birth and death rates are undeniably one of the most relevant terms to the causes of colony collapse. There are many external factors contributing to the increase in birth and death rates, for example, diseases and parasites. Therefore, knowing the minimum birth rate or maximum death rate of a colony before the collapse is crucial for implementing protective treatments. In this study, we conducted simulations of the population dynamics with respect to the average number of eggs laid per day and the death rates, respectively. The simulation results, after varying the average number of eggs laid per day, are shown in Figures 6(c) and (d), while the results from the death rate variation simulation are shown in Figures 7(a), (b), (c), and (d). The findings indicate that the honeybee colony becomes unsustainable when the egg-laying rate is lower than 1,130 eggs per day. Likewise, the colony will collapse when the immature worker and forager death rates exceed 12.3% per day and 11.4% per day, respectively. Figure 6(b), Figure 6(d), Figure 7(b) and (d) serve as indicators for determining the critical condition leading to the collapse of the honeybee colony, denoted by vertical blue lines.

3.1.2.3 Colony size cut-off threshold

Another relevant variable in our model is the colony size, $\sqrt{K}$, which is largely responsible for brood development rate and egg fertility. Accordingly, we analyzed the relevance of this variable by varying its value (10,000–79,000 honeybees), and visualizing the bee population dynamics as a 3–dimensional graph as shown in Figure 8(a) and as a corresponding time projection graph, shown in Figure 8(b). According to the simulation results, colonies with more than 98,742 honeybees are not able to maintain their integrity.

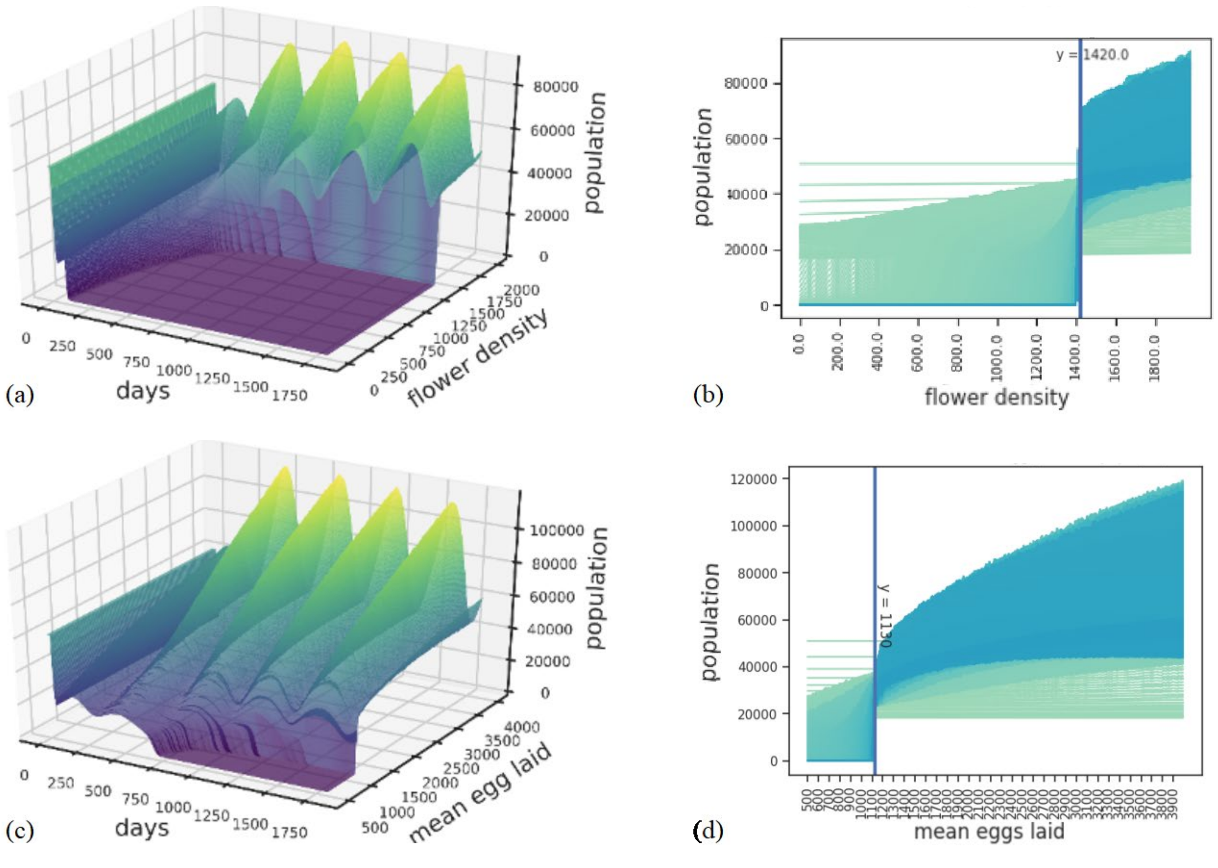

Figure 6. Graphs depicting (a) honeybee population dynamics and their (b) corresponding time projection with the colony collapse cut-off threshold in response to varying flower densities (0–2,000 flowers per square meter), and (c) the honeybee population dynamics and (d) their corresponding time projection with the colony collapse cut-off threshold for different maximal mean of eggs laid per day (1,000–4,000 eggs per day)

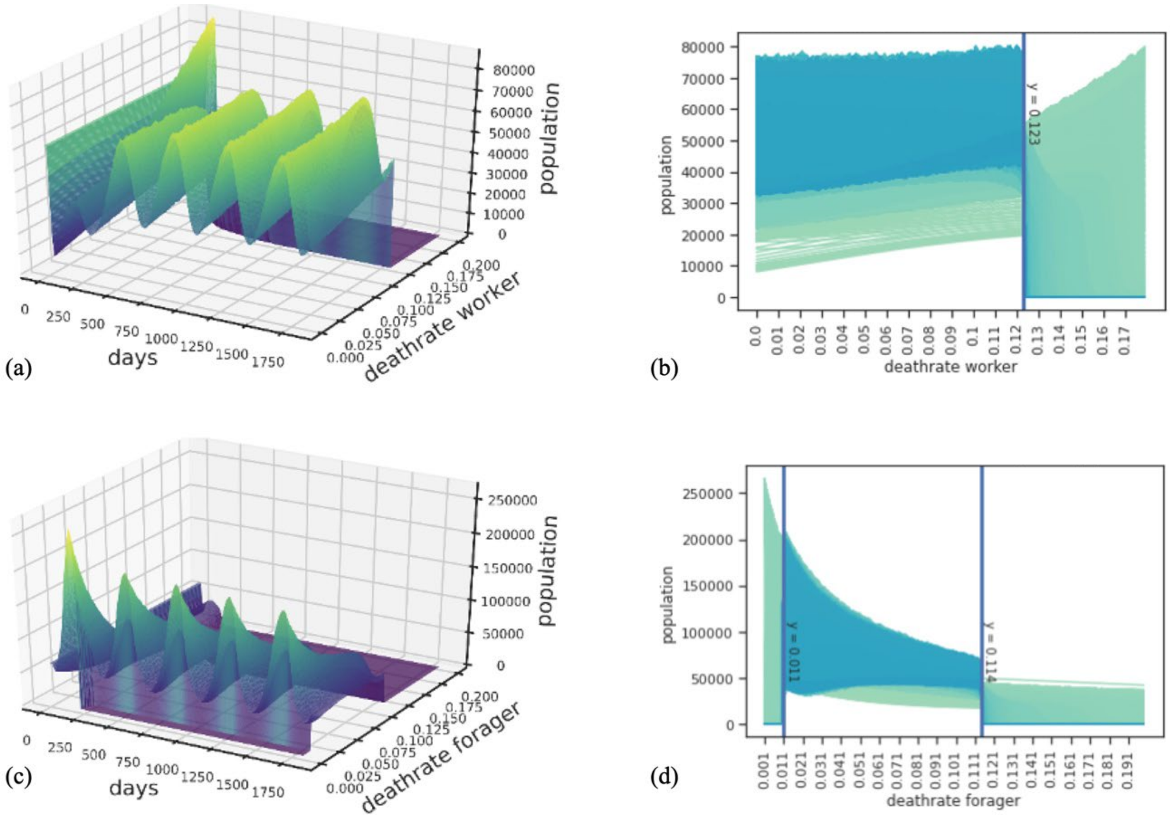

Figure 7. Graphs depicting (a) honeybee population dynamics and their (b) corresponding time projection with the colony collapse cut-off threshold in response to varying immature worker death rates (0.0–17.5% per day), and (c) honeybee population dynamics and (d) their corresponding time projection with the colony collapse cut–off threshold for different forager death rates (0–20% per day)

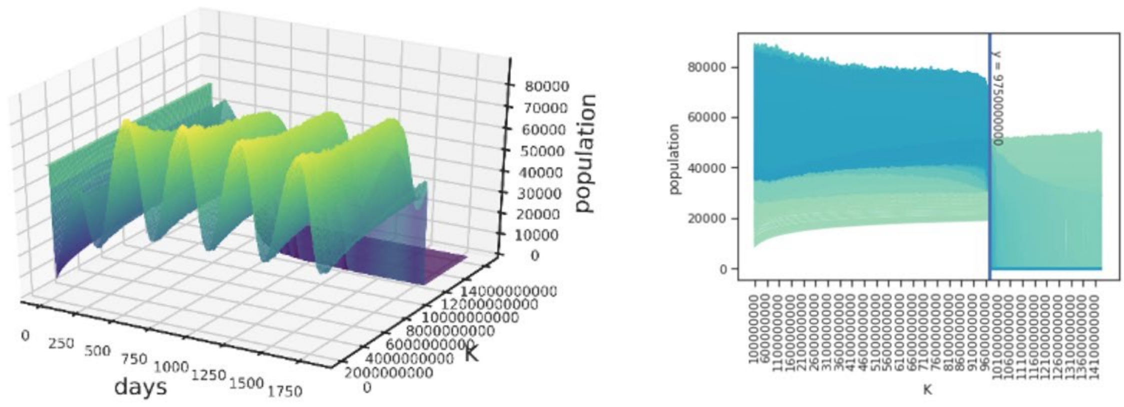

Figure 8. Graphs depicting honeybee population dynamics (left) and their corresponding time projection (right) with varying colony sizes (10,000–79,000 honeybees)

3.1.3 Seasonal impact degree cut-off threshold

Seasonal impact degree is an adjustable parameter, responsible for controlling the expressiveness of the seasonality in the region of interest. However, theoretically, the parameter should be readjusted whenever the model is used with a new environmental constraint. Therefore, we conducted a sensitivity analysis of the parameter to ascertain its significance in shaping the dynamics of the honeybee population. We varied the seasonal impact degree from 0.000–1.000 and visualized the outcome, as shown in Figure 9. The cut-off threshold of the seasonal impact degree was found to be 0.77.

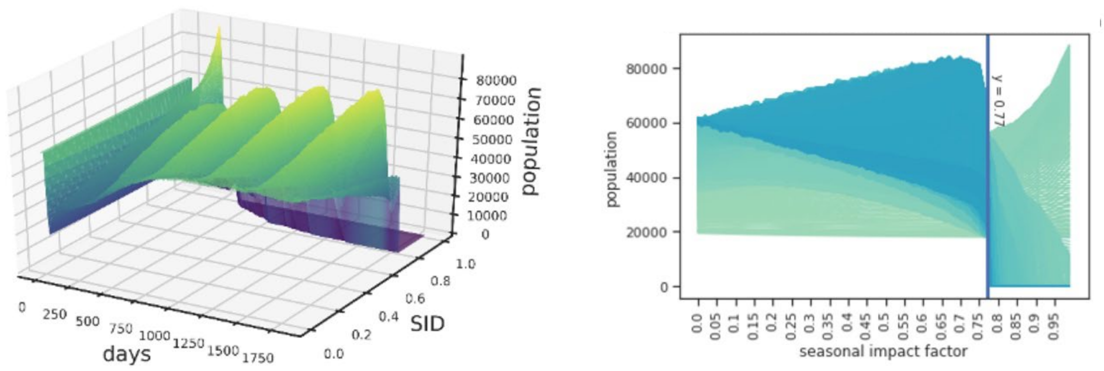

Figure 9. Graphs depicting the honeybee population dynamics (left) and their corresponding time projection (right) with varying seasonal impact degrees (0–1)

4. DISCUSSION

The strength of our model lies in its high adaptability, achieved through the segmentation of the bee life cycle stages. This segmentation enables us to predict rare, unpredictable events that specifically impact bees at certain life cycle stages to be predicted through minor adjustments. Additionally, the converting differential equations to difference equations reduces numerical simulation time, enabling a more efficient use of computational resources.

During the prediction of colony collapse, it became evident that each parameter possesses a varying degree of influence on the simulation. Notably, parameters such as egg-laying rate, flower density, and colony size at which brood survival rate is half maximum exhibit a linear relationship with the predicted population. However, the model demonstrates heightened sensitivity to the death rate, with colony viability confined to a narrower range of death rates. The impact of the death rate on the population follows a non-linear pattern, fitting a second-order regression equation.

Due to the absence of a definitive metric for converting population size to beehive weight, we employed the trend of honey storage within the hive as an alternative measure, correlating it with the beehive weight data from the previous research of Lecocq et al. (2015). The comparison yielded remarkable results, indicating a correlation between the amount of honey stored and the overall weight of the hive. Figure 10 illustrates the monthly predicted amount of honey, aligning with the observed fluctuations in measured hive weight over the year, thereby validating the model. The trend initiates at its lowest point, experiences a sharp incline throughout the year, and concludes with a slight decline.

Despite its strengths, the model does have certain limitations and opportunities for improvement. It does not account for extreme scenarios involving the destruction of hives by natural disasters or other animals. Furthermore, the model lacks a death rate coefficient associated with maintenance workload. The deconstruction of hives has a distinct impact on population dynamics, as workload distribution differs during hive reconstruction. Consequently, the model predictions may not align with real-world outcomes in these cases.

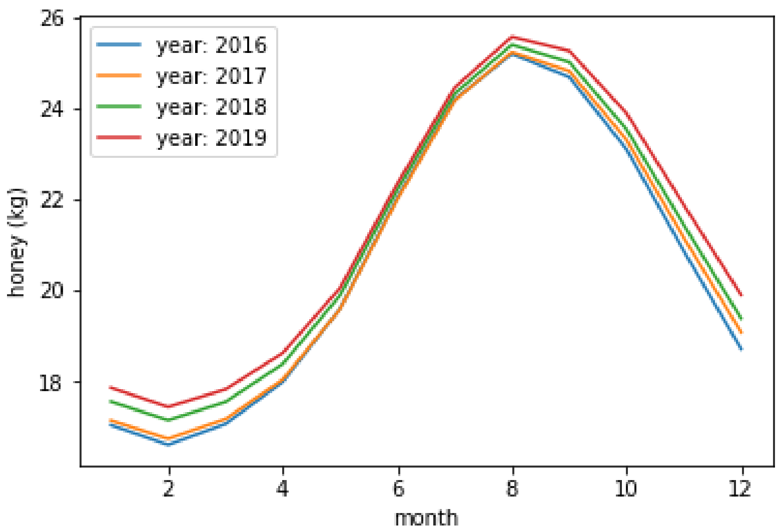

Figure 10. Amount of honey in the hive by month in a 4–year simulation

5. CONCLUSION

This research focused on modeling honeybee population dynamics and the quantity of honey within the colony using differential equations and numerical simulations. Based on our findings, the critical thresholds for various parameters were determined. These include a flower density cutoff of 1,420 flowers per square meter, an egg-laying rate of 1,130 eggs per day, an immature worker death rate of 12.3% per day, a forager death rate of 11.4%, a colony size of 98,742 honeybees, and a seasonal impact degree of 0.77, respectively. Notably, the impact of the egg-laying rate, flower density, colony size, and seasonal impact degree on the predicted honeybee population displayed a linear relationship, whereas the death rates exhibited a second-degree relationship.

Importantly, the simulation results align well with previous research, confirming the validity and reliability of our model.

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