

Dynamical analysis combined with parameter identification for a model of infection in honeybee colonies with social immunity

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Abstract: Several models on honeybee population dynamics have been considered in the past decades, which explain that the growth of bee colonies is highly dependent on the availability of food and social inhibition. The phenomenon of the Colony Collapse Disorder (CCD) and its exact causes remain unclear and here we are interested on the factor of social immunity.

We work with the mathematical model in [1]. The core model, consisting of four nonlinear ordinary differential equations with unknown functions: brood and nurses B , iB , N and iN represent the number of healthy brood, infected brood, healthy nurses, and infected nurses, respectively.

First, this model implements social segregation. High-risk individuals such as foragers are limited to contact only nectar-receivers, but not other vulnerable individuals (nurses and brood) inside the nest. Secondly, it includes the hygienic behavior, by which healthy nurses actively remove infected workers and brood from the colony.

We aim to study the dynamics and the long-term behavior of the proposed model, as well as to discuss the effects of crucial parameters associated with the model. In the first stage, we study the model equilibria stability

in dependence of the reproduction number.

In the second stage, we investigate the inverse problem of parameters identification in the model based on finite number time measurements of the population size. The conjugate gradient method with explicit Frechet derivative of the cost functional is proposed for the numerical solution of the inverse problem.

Computational results with synthetic and realistic data are performed and discussed.

Keywords: honeybee population dynamics, social immunity, least-squares fitting

I. INTRODUCTION

Over recent years, numerous mathematical frameworks have been formulated to analyze and forecast the population dynamics of honeybees.

In the study [1], the researchers devised a novel model focusing on the spread of diseases within bee colonies, primarily through trophallactic interactions. The model posits that an infection enters the colony

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when a foraging bee, having contracted the disease outside the hive, engages in nectar transfer through trophallaxis to a bee receiving nectar. This receiver bee then propagates the disease to other bees, encompassing both nurse bees and larvae. This model is broadly relevant to diseases that are spread through pathways related to food, particularly those presumed to be facilitated by trophallaxis.

The developed model incorporates several critical aspects that distinguish it from other prominent models in the field. Initially, it emphasizes the concept of social immunity, particularly highlighting the separation of bees into low-risk and high-risk groups, and the practices of hygiene directed at ill bees. This focus on social immunity has rarely been the primary consideration in other models, with only a few exceptions. Additionally, the model integrates the concept of hygienic behavior, wherein healthy nurse bees remove infected workers [2–4] and brood [5–7] from the colony. These two elements are central to the model’s representation of social immunity, playing a pivotal role in curbing the horizontal spread of pathogens among colony members.

The paper is organized as follows. In the next section, both the core and the extended model are presented. The nonnegativity and boundedness properties of the solution are studied in Section 3, while in the following section the equilibrium points are explored in detail. The reproduction number is explained and derived in Section 5. The solution to the inverse coefficient problem, which is the main novelty of the paper, is extendedly considered in Section 6. The following section contains the numerical simulations of the solutions, and the paper is concluded in the last section.

II. MATHEMATICAL MODELS

In this section, we present the models we will further investigate. First to discuss is the core model, which is later extended into a sophisticated counterpart, simply called the extended model.

A. Core model

We follow the modeling of paper [1], where the core model is

$$\frac{dB}{dt} = l_0 - \frac{1}{n_B} B - p_{t0} \cdot k_{NB} \cdot iN \cdot B, \quad (1)$$

$$\begin{aligned} \frac{diN}{dt} = & -\frac{1}{n_B} iB + p_{t0} \cdot k_{NB} \cdot iN \cdot B \\ & - k_{rem} \cdot iB \cdot N - k_d \cdot iB, \end{aligned} \quad (2)$$

$$\begin{aligned} \frac{dN}{dt} = & \frac{1}{n_B} \cdot B - \frac{1}{n_N} \cdot N - p_{t1} \cdot k_{RN} \cdot iR_1 \cdot N \\ & - p_{t,rem} \cdot k_{rem} \cdot iB \cdot N, \end{aligned} \quad (3)$$

$$\begin{aligned} \frac{diN}{dt} = & \frac{1}{n_B} \cdot iB - \frac{1}{n_N} \cdot iN + p_{t1} \cdot k_{RN} \cdot iR_1 \cdot N \\ & - k_{rem} \cdot iN \cdot N - k_d \cdot iN \\ & + p_{t,rem} \cdot k_{rem} \cdot iB \cdot N, \end{aligned} \quad (4)$$

where

$$\frac{dB}{dt} = \frac{d}{dt}(B), \quad \frac{diB}{dt} = \frac{d}{dt}(iB), \quad \text{etc.}$$

To formulate the mathematical model, we use the following assumptions [1]:

A1. Offspring originates from a consistent egg-laying rate represented by l_0 . Both uninfected and afflicted evolve into their corresponding nurse states, either uninfected or affected, at a rate given by $1/n_B$, where $n_B = 20$ days as referenced in [8, 9]. Uninfected and affected nurses further mature into their respective states of *nectar-collectors* at a rate given by $1/n_N$, where $n_N = 10$ days [10]. The main model does not account for nectar collectors and foragers, but they are incorporated in the extended model (next subsection).

A2. When providing nourishment, affected nurses pass the ailment to the offspring. The assumption is that the offspring are susceptible to the ailment at a rate represented by $p_{t0} \cdot k_{NB} \cdot iN$, where p_{t0} denotes the likelihood of ailment spread per interaction between an afflicted nurse and offspring, k_{NB} stands for the interaction rate between nurses and offspring, and iN signifies the count of afflicted nurses, as shown in (1), (2). In this context, the term *brood encompasses eggs, larvae, and pupae*, collectively for ease of representation.

A3. Uninfected nurses execute the removal of their affected counterparts. This action is described by healthy nurses (N) actively removing the infected ones (iN) from the group at a steady rate of k_{rem} , as depicted in (4).

A4. Healthy nurses (N) proactively extract infected offspring (iB) from their chambers at the same consistent rate k_{rem} as shown in (2). Though it is documented that bees aged 15-18 days predominantly perform this brood removal [5–7], evidence also indicates nurse bees’ involvement. This paper supposes that nurse bees have the capability to remove both infected offspring and fellow workers [2–4].

A5. Nurses risk infection when they come in contact with infected nectar-collectors. It is noted that these nectar-collectors engage in nectar-sharing interactions

with nurse bees during their visits to deposit nectar within the colony. The model (1)-(4) makes an assumption: the transmission rate of infection stands at $p_{t1} \cdot k_{RN} \cdot iR_1$. Here, p_{t1} represents the likelihood of disease spread during an encounter between an infected nectar-collector and a nurse; k_{RN} denotes the encounter rate, and iR_1 is the count of diseased nectar-collectors bearing nectar, elaborated in the extended model. In the core model (1)-(4) the value of $p_{t1} \cdot k_{RN} \cdot iR_1$ in eqs. (3) and (4) is perceived as a constant, set at 5×10^{-4} daily [1].

A6. The main assumption is that the primary pathway for transmitting infections is through nectar distribution, and nurses are not susceptible to infections from other infected nurse bees. Furthermore, the contagion is believed to propagate singularly from nectar donors to those receiving it.

A7. When hygienic bee workers engage in the removal of infected broods, they might contract the infection due to contact with the infected tissues. This probability is denoted as $p_{t,rem}$ in (3) and (4). Initially, the value for $p_{t,rem}$ is set at 0, and the scholars from [1] delved into this parameter through their numerical evaluations.

A8. The reaction of individual honeybees to infections can vary, influenced by the degree of the infection and other concurrent stressors. To illustrate, numerous viruses that affect honeybees do not manifest any noticeable symptoms. However, when these bees encounter additional stressors, the latent infection might escalate, intensifying honeybee mortality rates.

Colony Collapse Disorder (CCD), impacting honeybee populations, manifests as abrupt demise of colonies with an absence of living adult bees within the hive. This phenomenon is attributed to several contributing factors including emerging pathogens and pests, diminished genetic diversity, pesticide usage, lack of high-quality nourishment, and environmental shifts, as referenced in [10, 11].

This disorder notably impairs the navigational abilities of adult bees. They depart their hive for pollen collection but fail to return. Despite the presence of honey and pollen within the hive, and indications of recent breeding activities, the adult bee population vanishes.

Occasionally, the queen bee, along with a handful of surviving bees, may be found in the brood area. The presence of honey and pollen remains consistent in the hive, accompanied by signs of recent brood rearing. CCD is further distinguished by a delay in the plundering of honey from the deceased colonies

by neighboring, healthy bee colonies, and a slower incursion by typical pests such as wax moths or small beetles. Significantly, CCD seems to exclusively affect the European honeybee, *Apis mellifera* [12].

B. Extended model

Upon their return from gathering nectar, foragers distribute their collected nectar to worker bees in charge of food refinement through trophallaxis, known as nectar-receivers.

While the majority of these nectar receivers promptly store the nectar in honey chambers, a fraction distributes the nectar to secondary receivers, predominantly nurse bees. In the more detailed model, both nectar-receivers and foragers are further classified into distinct bee categories. Receivers can be categorized as either unloaded (R_0 and iR_0) or loaded with nectar (R_1 and iR_1). Similarly, foragers are categorized as unloaded (F_0 and iF_0) or loaded (F_1 and iF_1).

In the core model, both uninfected and infected nurses transition to become either uninfected or infected nectar-receivers without nectar in the broader model, respectively. Nectar-handlers transition into foragers at a consistent rate of $1/n_R$, given that n_R equates to 11 days [10]. Foragers retain their roles until they reach the end of their life cycle, at a rate concluded by $1/n_F$, with n_F being 14 days [10].

Unloaded foragers gather nectar and, subsequently, are classified as loaded at a steady rate represented by k . This rate encapsulates various actions, such as rallying, sourcing nectar, and re-entering the hive. It is assumed that foragers contract infections outside the confines of the hive. To represent the beginning of an infection within the colony, a singular infected forager is assumed to return from a nectar-gathering expedition at initial time, denoted as $iF_1(t_0) = 1$. Within the designated offloading zone, loaded foragers (F_1 or iF_1) pass on their nectar to unloaded (R_0 or iR_0) at a fixed rate, symbolized by k_{FR} , denoting the interaction frequency between foragers and nectar-handlers. Once foragers have dispensed their load, they pause before being prompted to gather more resources. Studies have indicated that foragers with infections exhibit significantly diminished navigational abilities when compared to their healthy counterparts. Consequently, it is assumed that these infected foragers have a survival probability, denoted as p_{surv} , in successfully returning to the colony during their foraging expeditions.

Nectar-receivers who are initially without nectar and then acquire it from foragers become loaded at a steady

rate, represented by k_{FR} . When a non-infected nectar-receiver acquires nectar from an infected forager, there exists a chance, marked as p_{t2} , that the former will contract the infection. Once loaded, nectar-receivers proceed to deposit the nectar in the hive's honey cells and then revert to an unloaded state at a consistent rate of $1/t_S$. In the process of storing nectar, these receivers often engage in feeding interactions with numerous nurse bees. An encounter between an infected nectar-receiver and a healthy nurse bee may lead to the transmission of the disease to the latter, with a transmission probability denoted as p_{t1} , (3) and (4).

Similar to the fundamental assumptions of the core model, transmission of the infection is believed to occur solely from nectar-donating to nectar-receiving bees. The full model integrates the core and extended models, where the infection rate of N in (3) and (4) is contingent on the quantity of infected nectar-receivers carrying loads (iR_1). In the extended model, mortality among infected receivers and foragers due to the disease is not considered, focusing instead on the non-lethal, subclinical infection of the colonies, hence assuming a death rate coefficient (k_d) of zero:

$$\begin{aligned} \frac{dR_0}{dt} &= \frac{N}{n_N} - \frac{R_0}{n_R} - k_{FR}(F_1 + iF_1)R_0 + \frac{R_1}{t_S}, \\ \frac{dR_1}{dt} &= -\frac{R_1}{n_R} + k_{FR}(F_1 + (1 - p_{t2})iF_1)R_0 - \frac{R_1}{t_S}, \\ \frac{d(iR_0)}{dt} &= \frac{iN}{n_N} - \frac{iR_0}{n_R} - k_{FR}(F_1 + iF_1)iR_0 + \frac{iR_1}{t_S}, \\ \frac{d(iR_1)}{dt} &= -\frac{iR_1}{n_R} - k_{FR}(F_1 + iF_1)iR_0 \\ &\quad + p_{t2}k_{FR}iF_1R_0 - \frac{iR_1}{t_S}, \\ \frac{dF_0}{dt} &= \frac{R_0}{n_R} - \frac{F_0}{n_F} + k_{FR}(R_0 + iR_0)F_1 - kF_0, \\ \frac{dF_1}{dt} &= \frac{R_1}{n_R} - \frac{F_1}{n_F} - k_{FR}(R_0 + iR_0)F_1 + kF_0, \\ \frac{d(iF_0)}{dt} &= \frac{iR_0}{n_R} - \frac{iF_0}{n_F} + k_{FR}(R_0 + iR_0)iF_1 - kiF_0, \\ \frac{d(iF_1)}{dt} &= \frac{iR_1}{n_R} - \frac{iF_1}{n_F} - k_{FR}(R_0 + iR_0)iF_1 \\ &\quad + p_{surv}kiF_0. \end{aligned} \tag{5}$$

III. NONNEGATIVITY AND BOUNDEDNESS

In this section we analyze the positivity and boundedness of the system variables to show the well-posedness of system (1)-(4).

Following [1], we have formulated a four compartment model (1)-(4) to analyze the segregation of worker bees and a hygienic response by which healthy nurse

bees exterminate infected bees to mitigate horizontal transmission of the infection to other bee members.

Let us introduce some notations in order to simplify the rewriting of the system (1)-(4).

Namely, we let:

$$\begin{aligned} x_1(t) &= B(t), \quad x_2(t) = iB(t), \\ x_3(t) &= N(t), \quad x_4(t) = iN(t), \\ p_0 &= p_{t0} \cdot k_{NB}, \quad k_r = k_{rem}, \quad b = \frac{1}{n_B}, \\ p_1 &= p_{t1} \cdot k_{RN} \cdot iR_1, \quad p_2 = p_{t,rem}, \quad n = \frac{1}{n_N}. \end{aligned}$$

Then, we rewrite the system (1)-(4) as follows

$$\begin{aligned} \frac{dx_1}{dt} &= l_0 - bx_1 - p_0x_1x_4 \\ &\equiv f_1(x_1, x_4), \end{aligned} \tag{6}$$

$$\begin{aligned} \frac{dx_2}{dt} &= -(b + k_d)x_2 + p_0x_1x_4 - k_rx_2x_3 \\ &\equiv f_2(x_1, x_2, x_3, x_4), \end{aligned} \tag{7}$$

$$\begin{aligned} \frac{dx_3}{dt} &= bx_1 - (n + p_1)x_3 - p_2k_rx_2x_3 \\ &\equiv f_3(x_1, x_2, x_3), \end{aligned} \tag{8}$$

$$\begin{aligned} \frac{dx_4}{dt} &= bx_2 + p_1x_3 - (n + k_d)x_4 + p_2k_rx_2x_3 \\ &\quad - k_rx_3x_4 \equiv f_4(x_2, x_3, x_4). \end{aligned} \tag{9}$$

In the following, we write the system (6)-(9) in the vector form

$$\begin{aligned} \frac{dx}{dt} &= f(x(t)), \quad x \equiv (x_1, x_2, x_3, x_4), \quad t \geq 0, \\ f(x(t)) &= \left(f_1(x(t)), f_2(x(t)), f_3(x(t)), f_4(x(t)) \right). \end{aligned} \tag{10}$$

System (10) is positive (short for 'non-negativity preserving') if

$$x(0) \geq 0 \implies x(t) \geq 0 \quad \forall t \geq 0.$$

Theorem 7.1 in [13] says that if the right-hand side $f(x)$ satisfies the Lipschitz condition, then the system is positive if for any vector $v \in \mathbb{R}^4$ and all $i = 1, 2, 3, 4$ we have the following results:

Theorem 1. Solutions of system (6)-(9) or (10) in \mathbb{R}_+^4 are positive for all final time $t \in (0, t_f)$.

Proof: The right-hand $f(x(t))$ of the system (10) is continuous and locally Lipschitzian on the space of continuous functions, from which it follows that there exists a unique solution $x(t)$ on a finite interval $[0, t_f]$, see e. g. [14]. We show that $x(t) > 0, \forall t \in [0, t_f)$.

Let us suppose that it does not hold, then $\exists t_1 \in [0, t_f)$ such that

$$x_1(t_1) = 0, \frac{dx_1}{dt}(t_1) \leq 0 \text{ and } x_1(t) > 0, \forall t \in [0, t_1).$$

Then, it follows from equation (6):

$$0 \geq \frac{dx_1}{dt}(t_1) = l_0 > 0 \implies \text{contradiction.}$$

Next, suppose that there exists $t_3 \in [0, t_f)$ such that

$$x_3(t_3) = 0, \frac{dx_3}{dt}(t_3) \leq 0 \text{ and } x_3(t) > 0, \forall t \in [0, t_3).$$

Then it follows from equation (8) and $x_1(t) > 0, t \in [0, t_1)$ that

$$0 \geq \frac{dx_3}{dt}(t_3) = b(x_1(t_3)) > 0 \implies \text{contradiction.}$$

Further, we show that $x_2(t) > 0$ for $t \in [0, t_f)$. If it does not hold, then $\exists t_2$ such that

$$x_2(t_2) = 0, \frac{dx_2}{dt}(t_2) \leq 0 \text{ and } x_2(t) > 0, \forall t \in [0, t_2).$$

So, it must be true that $x_4(t) \geq 0, \forall t \in [0, t_2)$. If it does not hold, then $\exists t_4 \in (0, t_3)$ such that

$$x_4(t_4) = 0, \frac{dx_4}{dt}(t_4) \leq 0 \text{ and } x_4(t) \geq 0, \forall t \in [0, t_4).$$

Then from the equation (9) we have:

$$0 \geq \frac{dx_4}{dt}(t_4) = bx_2(t_4) + p_1x_3(t_4) + p_2k_2x_2(t_4)x_3(t_4) > 0 \implies \text{contradiction.}$$

Therefore $x_4(t) > 0$ for $x \in [0, t_2)$. Now from equation (7) we have:

$$0 \geq \frac{dx_2}{dt}(t_2) = p_0x_1(t_2)x_4(t_2) > 0 \implies \text{contradiction.}$$

Corollary 1. *The total population $N(t) = \sum_{i=1}^4 x_i(t)$ is positive, if $x^i(0) > 0, i = 1, 2, 3, 4$ and $N(t) < C = \text{constant}$ for all $0 < t < \infty$.*

Proof: The positiveness of $N(t)$ directly follows from Theorem 1.

Next, summing the left-hand sides and the corresponding right-hand sides of the equation (6)-(9) and applying Theorem 1, we obtain:

$$\frac{dN}{dt} < l_0 - k_d x_2 - n x_3 - (n + k_d) x_4 \leq l_0 - (c - x_1),$$

where $c = \min(k_d, n, n + k_d) = \min(k_d, n)$.

Then, $N(t) \leq \tilde{N}(t)$, where

$$\begin{aligned} \frac{d\tilde{N}}{dt} + C\tilde{N} &= l_0 + c\tilde{x}_1(t), \quad \tilde{N}(0) = N(0), \\ \frac{d\tilde{x}_1}{dt} + b\tilde{x}_1 &= l_0, \quad \tilde{x}_1(0) = x_1(0). \end{aligned}$$

First, for \tilde{x}_1 we get

$$\tilde{x}_1(t) = \left(x_1(0) - \frac{l_0}{b}\right) e^{-bt} + \frac{l_0}{b},$$

then for $\tilde{N}(t)$ we find

$$\begin{aligned} \tilde{N}(t) &= l_0 \left(\frac{1}{c} + \frac{1}{b}\right) + \frac{c}{c-b} \left(x_1(0) - \frac{l_0}{b}\right) e^{-bt} \\ &+ \left[N(0) - l_0 \left(\frac{1}{c} + \frac{1}{b}\right) - \frac{c}{c-b} \left(x_1(0) - \frac{l_0}{b}\right)\right] e^{-ct} \end{aligned}$$

Since the constants b, c are positive, then $\tilde{N}(t) < C = \text{const}$. ■

IV. EQUILIBRIUM ANALYSIS

In this section we analyze the equilibrium points of system (1)-(4) along their stability conditions. For epidemiological models, usually basic reproduction number \mathcal{R}_0 (16) determines the existence of endemic equilibrium and stability of disease-free equilibrium of a system. System (6)-(9) (respectively (1)-(4)) has the following equilibrium points.

A. Disease-free equilibrium (DFE)

A disease-free equilibrium point is a solution to the system (1)-(4) in holding that there is no disease in the population. In this case $iB = iN = 0$ in (1)-(4), respectively $x_2 = x_4 = 0$ in (6)-(9). Therefore

$$E_0 = \left(\frac{l_0}{b}, 0, \frac{l_0}{n}, 0\right). \tag{11}$$

B. Endemic equilibrium (EE)

Using the definition of an equilibrium point, we solve the system of nonlinear algebraic equations of right hand-side of (6)-(9).

Using the proposed values of model parameters in [1], we have $p_{t,rem} = 0.0, k_d = 0.0 \text{ day}^{-1}$ and therefore in the system (6)-(9): $p_2 = 0, k_d = 0$. Now from (8) we find

$$x_1 = \frac{n + p_1}{b} x_3. \tag{12}$$

We substitute this expression for x_1 into (6) to obtain

$$x_4 = \frac{b}{p_0} \left(\frac{l_0}{n + p_1} \cdot \frac{1}{x_3} - 1\right). \tag{13}$$

Next, from the right hand side of (9) and using formulas (7), (8) we obtain:

$$x_2 = -\left(\frac{p_1}{b} + \frac{k_r}{p_0}\right)x_3 + \frac{nl_0}{p_0(n+p_1)} \cdot \frac{1}{x_3} + \frac{1}{p_0} \left(\frac{k_r l_0}{n+p_1} - n\right). \quad (14)$$

Finally, substituting (12)-(14) into (7), we get the cubic equation for x_3

$$Ax_3^3 + Bx_3^2 + Cx_3 + D = 0, \quad (15)$$

where

$$\begin{aligned} A &= k_r \left(\frac{p_1}{b} + \frac{k_r}{p_0}\right), \\ B &= -n - \frac{k_r}{p_0} \left(\frac{k_r l_0}{n+p_1} - b - n\right), \\ C &= -\frac{k_r l_0 (b+n)}{p_0(n+p_1)} + \frac{bn}{p_0} + l_0, \\ D &= -\frac{bnl_0}{p_0(n+p_1)}. \end{aligned}$$

Once the equation (15) is solved, we find x_1 from (12), x_4 from (13) and then x_2 from (14).

We now analyze the roots of equation (15) for positivity. Since always $A > 0$, we rewrite (15) in the short form

$$x_3^3 + px_3^2 + qx_3 + r = 0, \quad p = \frac{B}{A}, \quad q = \frac{C}{A}, \quad r = \frac{D}{A}.$$

Algorithm:

Step 1. Calculate $\Delta = -27r^2 + 18pqr - 4q^3 - 4p^3r + p^2q^2 \geq 0$ to ensure that all roots are positive (not necessarily distinctive).

The necessary and sufficient conditions for the positivity of the roots are

$$p < 0, \quad q > 0, \quad r < 0.$$

This follows from the fact that the coefficient in front of x_3^3 is $1 > 0$ and then we apply the Descartes' rule of signs.

We note that $r < 0$ is always true.

Step 2. At the second stage we calculate x_1, x_2, x_4 and find three, two or one equilibrium points.

V. REPRODUCTION NUMBER

The basic reproduction number, \mathcal{R}_0 , of an infectious disease is the average number of secondary cases generated by a single primary case in a fully susceptible population. \mathcal{R}_0 is the most widely epidemiological measurement of the transmission potential in a given population.

It is primary used as a threshold: if $\mathcal{R}_0 < 1$, then the disease will fade out of the population, but if $\mathcal{R}_0 > 1$ the disease persist and become epidemic to the population. Furthermore, the larger the magnitude of \mathcal{R}_0 , the faster the disease will spread and presumably the more difficult it would be to control.

There are different methods in which \mathcal{R}_0 can be calculated. \mathcal{R}_0 is defined as a spectral radius of the next generation matrix [15].

Here, terms that describe appearances of new infections in each compartment belong in F , and the other terms belong in V . The Jacobian matrices obtained by differentiating F and V with respect to the relevant subset of variables are computed and evaluated at an equilibrium point, resulting the matrices JF u JF , respectively. So, the basic reproduction number, \mathcal{R}_0 , is defined as the spectral radius of the matrix $JF(JV)^{-1}$.

So, we represent the system (10) in the form

$$\frac{dx}{dt} = F(x) - V(x),$$

where

$$\begin{aligned} F(x) &= \begin{pmatrix} p_0x_1x_4 \\ p_1x_3 \end{pmatrix}, \\ V(x) &= \begin{pmatrix} bx_2 + k_r x_2 x_3 \\ -bx_2 + nx_4 + k_r x_3 x_4 \end{pmatrix}, \\ JF(x) &= \begin{pmatrix} 0 & p_0x_1 \\ 0 & 0 \end{pmatrix}, \\ JV(x) &= \begin{pmatrix} b + k_r x_3 & 0 \\ -b & n + k_r x_3 \end{pmatrix}. \end{aligned}$$

Then,

$$\begin{aligned} JF(E_0) &= \begin{pmatrix} 0 & p_0 \frac{l_0}{b} \\ 0 & 0 \end{pmatrix}, \\ JV(E_0) &= \begin{pmatrix} b + k_r \frac{l_0}{n} & 0 \\ -b & n + k_r \frac{l_0}{n} \end{pmatrix}, \end{aligned}$$

and eventually

$$\mathcal{R}_0 = \frac{l_0 n^2 p_0}{(n^2 + l_0 k_r)(bn + l_0 k_r)}. \quad (16)$$

VI. SOLUTION TO THE COEFFICIENT INVERSE PROBLEM

When we solve the problem (6)-(9) with the respective initial conditions, knowing the values of all coefficients, we actually solve the *direct* problem. In practice, though, we do not know the values of some parameters, since they cannot be measured directly and obtained in some way, even reasonably approximated. However, we are able to measure the functions B ,

iB, N, iN , since they represent the number of bees, belonging to the respective class, and could be counted by means of special hardware.

Before defining the observations, we are interested in the values of parameters $\mathbf{p} = (p_0, p_1, p_2, k_r, k_d)$, since they vary [1] and cannot be approximated. Their values could be bounded to belong to the admissible set $\mathbf{p} \in \mathbb{S}_{\text{adm}} = \{\mathbf{p} \in \mathbb{R}^5, 0 \leq p^j < P^j, j = \overline{1, 5}\}$, and the values P^j come from biological reasoning. Let $\mathbf{p} \in \mathbb{S}_{\text{adm}}$ and all solutions $x_i(t; \mathbf{p}), i = \overline{1, 4}$ be defined on $0 \leq t \leq T$. Now, we define the observations in the form

$$\begin{aligned} x_1^{\text{obs}}(t_k; \mathbf{p}) &= W_k, \quad x_2^{\text{obs}}(t_k; \mathbf{p}) = X_k, \\ x_3^{\text{obs}}(t_k; \mathbf{p}) &= Y_k, \quad x_4^{\text{obs}}(t_k; \mathbf{p}) = Z_k, \quad k = \overline{1, K}. \end{aligned} \quad (17)$$

The solution to the *inverse* problem consists of reconstructing the system (6)-(9) and the values of the parameters \mathbf{p} , using the additional data (17). To solve it, we employ the adjoint equation optimization method [16, 17].

In order to derive the *implied* values of the parameters, we will minimize the following quadratic cost functional

$$\begin{aligned} J(\mathbf{p}) &= J(p_0, p_1, p_2, k_r, k_d) \\ &= J_1(\mathbf{p}) + J_2(\mathbf{p}) + J_3(\mathbf{p}) + J_4(\mathbf{p}), \end{aligned} \quad (18)$$

where

$$\begin{aligned} J_1(\mathbf{p}) &= \sum_{k=1}^K (x_1(t_k; \mathbf{p}) - W_k)^2, \\ J_2(\mathbf{p}) &= \sum_{k=1}^K (x_2(t_k; \mathbf{p}) - X_k)^2, \\ J_3(\mathbf{p}) &= \sum_{k=1}^K (x_3(t_k; \mathbf{p}) - Y_k)^2, \\ J_4(\mathbf{p}) &= \sum_{k=1}^K (x_4(t_k; \mathbf{p}) - Z_k)^2. \end{aligned}$$

Using the gradient method [18], we solve the inverse problem.

Theorem 2. *The gradient $J'(\mathbf{p}) = (J'_{p_0}, J'_{p_1}, J'_{p_2}, J'_{k_r}, J'_{k_d})$ of the functional $J(\mathbf{p})$ (18) is defined as follows*

$$\begin{aligned} J'_{p_0}(\mathbf{p}) &= \int_0^T (\varphi_1 - \varphi_2)x_1x_4dt, \\ J'_{p_1}(\mathbf{p}) &= \int_0^T (\varphi_3 - \varphi_4)x_3dt, \end{aligned}$$

$$\begin{aligned} J'_{p_2}(\mathbf{p}) &= \int_0^T (\varphi_3 - \varphi_4)k_r x_2 x_3 dt, \\ J'_{k_r}(\mathbf{p}) &= \int_0^T (\varphi_2 + p_2(\varphi_3 - \varphi_4))x_2 x_3 + \varphi_4 x_3 x_4 dt, \\ J'_{k_d}(\mathbf{p}) &= \int_0^T \varphi_2 x_2 + \varphi_4 x_4 dt, \end{aligned} \quad (19)$$

where the auxiliary functions $\varphi_i, i = \overline{1, 4}$ are the unique solution to the adjoint final-value problem

$$\begin{aligned} \frac{d\varphi_1}{dt} &= \varphi_1(b + p_0x_4) - \varphi_2p_0x_4 - \varphi_3b \\ &\quad + 2 \sum_{k=1}^K (x_1(t; \mathbf{p}) - W(t))^2 \delta(t - t_k), \\ \frac{d\varphi_2}{dt} &= \varphi_2(b + k_d + k_r x_3) + \varphi_3 p_2 k_r x_3 \\ &\quad - \varphi_4(b + p_2 k_r x_3) \\ &\quad + 2 \sum_{k=1}^K (x_2(t; \mathbf{p}) - X(t))^2 \delta(t - t_k), \\ \frac{d\varphi_3}{dt} &= \varphi_2 k_r x_2 + \varphi_3(n + p_1 + p_2 k_r x_2) \\ &\quad - \varphi_4(p_1 + p_2 k_r x_2 - k_r x_4) \\ &\quad + 2 \sum_{k=1}^K (x_3(t; \mathbf{p}) - Y(t))^2 \delta(t - t_k), \\ \frac{d\varphi_4}{dt} &= (\varphi_1 - \varphi_2)p_0 x_1 + \varphi_4(n + k_d + k_r x_3) \\ &\quad + 2 \sum_{k=1}^K (x_4(t; \mathbf{p}) - Z(t))^2 \delta(t - t_k), \\ \varphi_i(T) &= 0, \quad i = \overline{1, 4}, \end{aligned} \quad (20)$$

where $\delta(\cdot)$ is the Dirac delta function.

Proof: Let us designate $\delta\mathbf{p} = (\delta p_0, \delta p_1, \delta p_2, \delta k_r, \delta k_d)^\top$, $\delta p_0 = \varepsilon h_1$, $\delta p_1 = \varepsilon h_2$, $\delta p_2 = \varepsilon h_3$, $\delta k_r = \varepsilon h_4$, $\delta k_d = \varepsilon h_5$ and $\delta x_i(t; \mathbf{p}) = x_i(t; \mathbf{p} + \delta\mathbf{p}) - x_i(t; \mathbf{p})$ for $i = \overline{1, 4}$. If we write the system (6)-(9) at $\mathbf{p} + \delta\mathbf{p}$, i. e., a system for $\{x_i(t; \mathbf{p} + \delta\mathbf{p})\}, i = \overline{1, 4}$ with the same initial conditions, and perform the differences between these two systems, we will arrive at a system for $\delta x_i(t; \mathbf{p}), i = \overline{1, 4}$ with zero initial data. Actually, the system is

$$\begin{aligned} \frac{d}{dt} \delta x_1 &= -b\delta x_1 - p_0 x_1 \delta x_4 - p_0 \delta x_1 x_4 - \delta p_0 x_1 x_4 \\ &\quad + \mathcal{O}(\delta \cdot), \\ \frac{d}{dt} \delta x_2 &= -(b + k_d)\delta x_2 - \delta k_d x_2 + p_0 x_1 \delta x_4 \\ &\quad + p_0 \delta x_1 x_4 + \delta p_0 x_1 x_4 - k_r \delta x_2 x_3 \\ &\quad - k_r x_2 \delta x_3 - \delta k_r x_2 x_3 + \mathcal{O}(\delta \cdot), \end{aligned}$$

$$\begin{aligned} \frac{d}{dt}\delta x_3 &= b\delta x_1 - (n + p_1)\delta x_3 - \delta p_1 x_3 - p_2 k_r x_2 \delta x_3 \\ &\quad - p_2 k_r \delta x_2 x_3 - p_2 \delta k_r x_2 x_3 - \delta p_2 k_r x_2 x_3 \\ &\quad + \mathcal{O}(\delta \cdot), \\ \frac{d}{dt}\delta x_4 &= b\delta x_2 + p_1 \delta x_3 + \delta p_1 x_3 - n\delta x_4 - k_d \delta x_4 \\ &\quad - \delta k_d x_4 + p_2 k_r x_2 \delta x_3 + p_2 k_r \delta x_2 x_3 \\ &\quad + p_2 \delta k_r x_2 x_3 + \delta p_2 k_r x_2 x_3 - k_r x_3 \delta x_4 \\ &\quad - k_r \delta x_3 x_4 - \delta k_r x_3 x_4 + \mathcal{O}(\delta \cdot). \end{aligned}$$

The increment of the functional $\delta J(\mathbf{p}) = J(\mathbf{p} + \delta \mathbf{p}) - J(\mathbf{p})$ in integral form could be written as [19]

$$\begin{aligned} \delta J(\mathbf{p}) &= 2 \sum_{k=1}^K \int_0^T (\delta x_1(t; \mathbf{p})(x_1(t; \mathbf{p}) - W(t))\delta(t - t_k) \\ &\quad + \delta x_2(t; \mathbf{p})(x_2(t; \mathbf{p}) - X(t))\delta(t - t_k) \\ &\quad + \delta x_3(t; \mathbf{p})(x_3(t; \mathbf{p}) - Y(t))\delta(t - t_k) \\ &\quad + \delta x_4(t; \mathbf{p})(x_4(t; \mathbf{p}) - Z(t))\delta(t - t_k)) dt \\ &\quad + \mathcal{O}(\varepsilon), \end{aligned} \tag{21}$$

where $\delta(\cdot)$ is the Dirac delta function.

As the fundamental idea of the adjoint equation method [16], we multiply the equations for $\frac{d}{dt}\delta x_i$, respectively, by smooth functions $\varphi_i(t)$ s. t. $\varphi_i(T) = 0$ for $i = \overline{1, 4}$, integrate both sides of the result from 0 to T and sum them up. On the other hand, if we integrate the left-hand side by parts and make use of $\delta x_i(0) = 0$, $\varphi_i(T) = 0$ for $i = \overline{1, 4}$, then

$$\int_0^T \sum_{i=1}^4 \varphi_i \frac{d}{dt} \delta x_i dt = - \sum_{i=1}^4 \int_0^T \delta x_i \frac{d\varphi_i}{dt} dt. \tag{22}$$

So, placing the expressions for $\frac{d\varphi_i}{dt}$ from (20) in (22) and taking into account (21), after some algebra we obtain

$$\begin{aligned} \delta J(\mathbf{p}) &= \delta p_0 \int_0^T (\varphi_1 - \varphi_2) x_1 x_4 dt \\ &\quad + \delta p_1 \int_0^T (\varphi_3 - \varphi_4) x_3 dt + \delta k_d \int_0^T \varphi_2 x_2 + \varphi_4 x_3 dt \\ &\quad + \delta k_r \int_0^T (\varphi_2 + p_2(\varphi_3 - \varphi_4)) x_2 x_3 + \varphi_4 x_3 x_4 dt \\ &\quad + \delta p_2 \int_0^T (\varphi_3 - \varphi_4) k_r x_2 x_3 dt + \mathcal{O}(\varepsilon). \end{aligned}$$

If we set $h_2 = h_3 = h_4 = h_5 = 0$, divide both sides by εh_1 and pass to the limit $\varepsilon \rightarrow 0$, we arrive at the formula for J'_{p_0} in (19). The other formulae are obtained analogously. ■

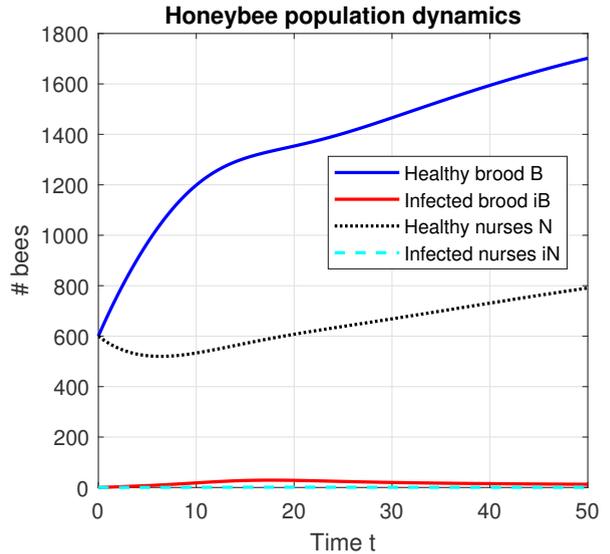


Fig. 1: Solution to the direct problem (6)-(9).

VII. COMPUTATIONAL SIMULATIONS

In this section, we provide numerical tests to verify the quality of the proposed algorithm. First we test the direct problem for the core and full model, and then we proceed to the inverse problem.

A. Direct problem

We solve the problem (6)-(9) with initial condition $x_1(0) = 600$, $x_2(0) = 0$, $x_3(0) = 600$, $x_4(0) = 0$. The infection is implicitly introduced via iR_1 , which takes part in p_1 . The values are accordingly [1] $l_0 = 120$, $b = 1/20$, $n = 1/10$, $p_0 = 0.03$, $p_1 = 0.0005$, $p_2 = 0$, $k_r = 0.0025$, $k_d = 0$. In this case, $\mathcal{R}_0 = 0.3808$.

We are interested in the near future up to $T = 50$ days. The results are plotted on Fig. 1.

Then, we solve problem (5) with initial data $R_0(0) = 700$, $R_1(0) = 0$, $iR_0(0) = 0$, $iR_1(0) = 0$, $F_0(0) = 900$, $F_1(0) = 0$, $iF_0(0) = 0$, $iF_1(0) = 2$. It means that at the first flight, two foragers get infected and transfer the disease through contact. The parameter values are $n_R = 11$, $n_F = 14$, $k_{FR} = 1.44$, $t_S = 0.01$, $p_{t2} = 0.3$, $k = 0.5$, $p_{surv} = 0$. The results are shown on Fig. 2.

B. Inverse problem

Now we aim to recover the parameters \mathbf{p} , using the observations (17). The other parameters stay the same, and the initial approximation to \mathbf{p} is $\mathbf{p}_{init} = \{0.05, 0.001, 0.001, 0.01, 0.001\}$. We suggest taking measurements equidistantly, one at every 10 days. This is very scarce observation, since the hardware could obtain measurements between minutes or even seconds.

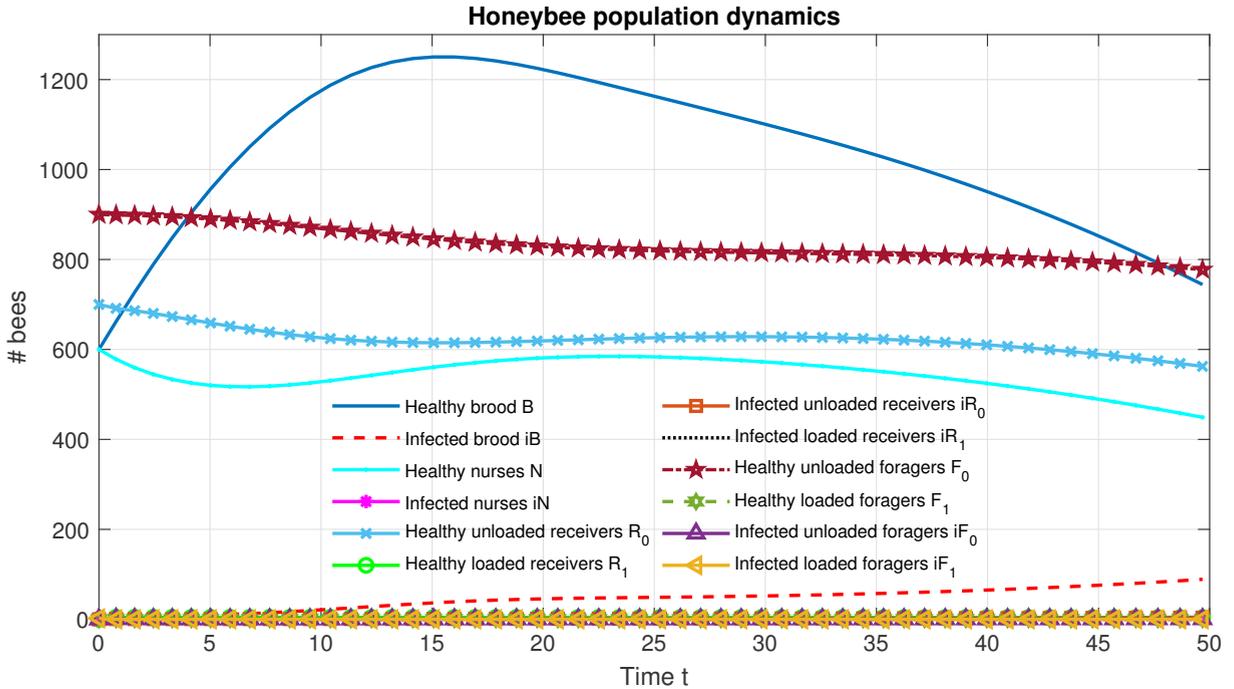


Fig. 2: Solution to the direct problem (5).

Table I: Identification of \mathbf{p} .

Par	p_{init}^j	p^j	\check{p}^j	$ p^j - \check{p}^j $	$\frac{ p^j - \check{p}^j }{p^j}$
p_0	0.05	0.03	0.0300	7.2103e-12	2.4034e-10
p_1	0.001	0.0005	5.0000e-4	8.7792e-14	1.7558e-10
p_2	0.001	0	2.2279e-14	2.2279e-14	—
k_r	0.01	0.0025	0.0025	6.2053e-13	2.4821e-10
k_d	0.001	0	2.3357e-14	2.3357e-14	—

The true and implied values of the parameters and their errors are displayed in Table I. With $\check{\mathbf{p}}$ it is denoted the estimator, i. e. the implied values after the minimization of J (18).

The reconstructed values practically coincide with the real ones. The errors are negligibly small. The values of the residuals $J_1(\check{\mathbf{p}}) = 3.0341e-17$, $J_2(\check{\mathbf{p}}) = 1.0730e-16$, $J_3(\check{\mathbf{p}}) = 9.7635e-18$, $J_4(\check{\mathbf{p}}) = 1.7697e-19$ are extremely small. All of these unequivocally demonstrate that the minimization is successful and the unknown parameters are accurately recovered.

VIII. CONCLUSION

Over the years, numerous models have been developed to comprehend the intricate dynamics of honeybee

populations. Central to these models is the understanding that the prosperity of bee colonies is significantly tethered to factors like food availability and social interactions. A particularly concerning anomaly observed in these colonies is the Colony Collapse Disorder. Despite intensive research, the exact triggers of this disorder remain enigmatic, leading us to explore the role of social immunity in this context.

The mathematical model we adopted is underpinned by four nonlinear ordinary differential equations, representing various bee categories within a colony, from healthy brood and nurses to their infected counterparts.

Two pivotal mechanisms are encapsulated within this model:

- 1) Social Segregation: To mitigate the spread of infections, the model limits high-risk bees, like foragers, to interact solely with nectar-receivers. This strategic restriction safeguards the more susceptible members of the colony, namely the nurses and brood.
- 2) Hygienic Behavior: In a bid to enhance the colony's resilience against infections, healthy nurse bees proactively identify and oust infected peers and brood, reinforcing the colony's natural defense mechanisms.

Our research endeavors focused on unpacking the intricacies of this model. We were keen to delve deep

into its dynamics, its long-term implications, and to discern the impacts of key parameters integral to the model.

Firstly, we meticulously analyzed the model equilibria stability. By evaluating equilibrium points in relation to the reproduction number, we gained invaluable insights into how the model reacts under varying conditions.

Our subsequent phase pivoted to a more sophisticated challenge – deciphering the inverse problem of parameter identification. Employing the conjugate gradient method, coupled with the explicit Frechet derivative of the cost functional, we charted a course to a numerical solution for this inverse problem.

Our computational simulations lead to findings not only validating our methodologies but also offering profound insights into the inner workings of honeybee colonies, particularly in the context of social immunity. As the global community grapples with the mysteries of the CCD, studies like ours illuminate potential pathways to safeguard these vital pollinators.

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