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Threshold Dynamics of Honey Bee Colonies with General Eclosion and Social Inhibition

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Abstract

Honey bee colonies are important to worldwide agriculture and the health of natural ecosystems. Understanding the factors behind colony persistence and failure has been a major challenge for both ecologists and mathematicians. In this paper, we present a general mathematical model to explore the threshold dynamics of honey bee colonies. We explicitly define the basic reproduction number in terms of model parameters and demonstrate its critical role in determining whether a colony survives or collapses. We offer a biological interpretation of the basic reproduction number and prove the threshold dynamics for the general model system. Our results are established using dynamical systems techniques, including the comparison principle, persistence theory, linearization, and global analysis. For specifically chosen eclosion and social inhibition functions, we perform a sensitivity analysis to determine how the basic reproduction number depends on the model parameters.

Keywords: honey bee colonies; threshold dynamics; basic reproduction number; equilibrium; stability

MSC: 92D25; 37N25; 34D23



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1. Introduction

Honey bees (*Apis mellifera*) play a vital role in global agriculture and natural ecosystems by providing essential pollination services [1]. However, honey bee populations in North America and the United Kingdom have been in decline since the 1940s [2–4]. According to the USDA National Agricultural Statistics Service [5], there were 4.3 million honey-producing colonies in 1976 and 3.3 million in 1989. In contrast, the figures for the most recent five years (2020–2024) were 2.71, 2.70, 2.67, 2.51, and 2.60 million, respectively. Over the past two decades, researchers have investigated the causes underlying honey bee colony failures [6]. In [7], the authors develop a mathematical model to investigate how variations in food availability interact with forager mortality to affect colony growth. The population dynamics of honey bee colonies are examined in [8] using both smooth and non-smooth modeling approaches.

The complexity and nonlinearities of the aforementioned models pose significant challenges for the mathematical analysis of honey bee dynamics. Therefore, it is essential to employ dynamical systems theory to examine the effects of key factors on the persistence or collapse of honey bee colonies. The aim of this study is to establish a mathematical framework for investigating the population dynamics of honey bee colonies. A crucial step

in this framework is the definition of a biologically meaningful threshold parameter, the basic reproduction number. In ecological systems, the value of this parameter determines whether a population persists or becomes extinct, whereas in epidemiological models, it serves as a key indicator of whether a disease will persist or disappear.

In this study, we use a general mathematical model to analyze the threshold dynamics that govern honey bee colony survival. In particular, we derive a critical threshold parameter that determines whether a colony will collapse or persist over time. The worker population of the honey bee is divided into two groups: hive bees, which carry out various tasks inside the nest, such as raising brood, and forager bees, which specialize in collecting food and materials [9]. Hence, we propose the following two-compartmental model of honey bee colonies:

$$H'(t) = b(H(t), F(t)) - (d + \alpha)H(t) + r(H(t), F(t)), \quad (1)$$

$$F'(t) = \alpha H(t) - mF(t) - r(H(t), F(t)), \quad (2)$$

where $H(t)$ and $F(t)$, respectively, denote the populations of hive bees and forager bees at time t . The eclosion rate is given by a general nonlinear function $b(H, F)$. The death rates of the hive bees and forager bees are d and m , respectively. The transition rate from hive bees to forager bees is α . The social inhibition is modeled by the nonlinear function $r(H, F)$. The hive-to-forager transition and social inhibition enhance colony growth, development, and environmental adaptation [10].

We adopt the following notations throughout this paper. We use $\mathbb{R}_+ = [0, \infty)$ to denote the set of non-negative real numbers. For any positive integer n , the set of non-negative vectors is denoted by $\mathbb{R}_+^n$. We say a vector $v \in \mathbb{R}_+^n$ is positive if each element of v is positive. If $g \in C^1(\mathbb{R}_+^2, \mathbb{R})$ is a differential function with two variables x and y , then we denote the partial derivative functions as follows:

$$g_1 = \partial_x g, \quad g_2 = \partial_y g.$$

If $g \in C^2(\mathbb{R}_+^2, \mathbb{R})$ is second-order differentiable, then we denote the second-order partial derivative functions as follows:

$$g_{11} = \partial_{xx}^2 g, \quad g_{12} = \partial_{xy}^2 g, \quad g_{21} = \partial_{yx}^2 g, \quad g_{22} = \partial_{yy}^2 g.$$

Clearly, we have $g_{12} = g_{21}$. For a square matrix $M \in \mathbb{R}^{n \times n}$, the spectral radius and the determinant of M are denoted as $\rho(M)$ and $\det(M)$, respectively. Let $\lambda_1, \dots, \lambda_n$ be the eigenvalues (counting multiplicity) of M , we have the following:

$$\rho(M) = \max_{1 \leq j \leq n} |\lambda_j|, \quad \det(M) = \prod_{j=1}^n \lambda_j.$$

We shall make some basic biological assumptions on our model system. First, the constants d , m and α are positive. Next, the initial values $H(0)$ and $F(0)$ are non-negative with $H(0) + F(0) > 0$. Finally, we assume that the functions $b(x, y)$ and $r(x, y)$ satisfy the following conditions:

(C1) $b \in C^2(\mathbb{R}_+^2, \mathbb{R}_+)$ with $b(0, 0) = 0$, $b(x, y) \leq L$, $b_1(x, y) \geq 0$ and $b_2(x, y) \geq 0$ for $(x, y) \in \mathbb{R}_+^2$.

(C2) $r \in C^2(\mathbb{R}_+^2, \mathbb{R}_+)$ with $r(x, 0) = 0$, $r_1(x, y) \leq 0$ and $r_2(x, y) \geq 0$ for $(x, y) \in \mathbb{R}_+^2$.

The biological interpretations of conditions (C1)–(C2) are as follows. No eclosion occurs if both hive bees and forager bees are absent. The eclosion rate increases with the populations of hive bees and forager bees; however, it is bounded above by a maximal rate

L . The social inhibition rate rises with the population of forager bees and decreases with the population of hive bees, and no social inhibition occurs in the absence of forager bees.

2. Results

2.1. Positiveness and Ultimate Boundedness

Proposition 1. Assume (C1)–(C2). The system (1) and (2) with positive initial values possesses a global unique solution $(H(t), F(t)) \in \mathbb{R}_+^2$ that is positive for all $t \geq 0$. Moreover, we have the following:

$$\limsup_{t \rightarrow \infty} [H(t) + F(t)] \leq \frac{L}{\min\{d, m\}};$$

that is, the solution is ultimately bounded by a constant independent of the initial values.

Proof. Given any positive initial values $H(0) > 0$ and $F(0) > 0$, we apply the standard theory of ordinary differential equations to obtain that the solution exists on a maximal interval $[0, T)$, where either $T = \infty$ or $|H(t)| + |F(t)| \rightarrow \infty$ as $t \rightarrow T^-$.

First, we claim that $H(t) > 0$ and $F(t) > 0$ for all $t \in [0, T)$. If not, then there exists $t_1 \in (0, T)$ such that $H(t)F(t) \neq 0$ for $t \in [0, t_1)$ and $H(t_1)F(t_1) = 0$. By continuity of the solution, we have $H(t) > 0$ and $F(t) > 0$ for all $t \in [0, t_1)$. Hence, the conditions (C1)–(C2) imply that $b(H(t), F(t)) + r(H(t), F(t)) \geq 0$ for all $t \in [0, t_1)$. Now, we obtain the following from (1):

$$\begin{aligned} 0 &\leq \int_0^{t_1} e^{(d+\alpha)t} [b(H(t), F(t)) + r(H(t), F(t))] dt \\ &= \int_0^{t_1} e^{(d+\alpha)t} [H'(t) + (d + \alpha)H(t)] dt \\ &= e^{(d+\alpha)t_1} H(t_1) - H(0). \end{aligned}$$

Since $H(0) > 0$, we have $H(t_1) > 0$. From the choice of t_1 we obtain $F(t_1) = 0$. It then follows from (2) and (C2) that $F'(t_1) = \alpha H(t_1) > 0$. Recall that $F(t) > 0$ for $t \in [0, t_1)$. We obtain $F(t_1) > 0$, which is a contradiction. Hence, we have proved that the solution remains positive for all $t \in [0, T)$.

Next, we add the two Equations (1) and (2) and make use of (C1) to find the following:

$$H'(t) + F'(t) = b(H(t), F(t)) - dH(t) - mF(t) \leq L - \mu[H(t) + F(t)],$$

where $\mu := \min\{m, d\} > 0$. In particular, $H(t) + F(t) \leq H(0) + F(0) + Lt$ for all $t \in [0, T)$, which implies that the solution cannot blow up at finite time. Hence, $T = \infty$. Moreover, the above differential inequality implies that

$$\limsup_{t \rightarrow \infty} [H(t) + F(t)] \leq \frac{L}{\mu}.$$

This completes the proof. $\square$

2.2. Basic Reproduction Number

On account of (C1)–(C2), our model system (1) and (2) possesses a trivial equilibrium $E_0 = (0, 0)$. We linearize the system about this trivial equilibrium and obtain the following:

$$\begin{pmatrix} H'(t) \\ F'(t) \end{pmatrix} = A \begin{pmatrix} H(t) \\ F(t) \end{pmatrix}, \quad A = \begin{pmatrix} b_1(0, 0) - (d + \alpha) + r_1(0, 0) & b_2(0, 0) + r_2(0, 0) \\ \alpha - r_1(0, 0) & -m - r_2(0, 0) \end{pmatrix}. \quad (3)$$

We split $A = B - V$, where the following is then calculated:

$$B = \begin{pmatrix} b_1(0,0) & b_2(0,0) \\ 0 & 0 \end{pmatrix}, \quad V = \begin{pmatrix} d + \alpha - r_1(0,0) & -r_2(0,0) \\ -\alpha + r_1(0,0) & m + r_2(0,0) \end{pmatrix}. \quad (4)$$

In view of (C1)–(C2), this is a regular splitting [11] in the sense that B is a non-negative matrix and V is a nonsingular matrix with a non-negative inverse, written as follows:

$$V^{-1} = \frac{1}{\det(V)} \begin{pmatrix} m + r_2(0,0) & r_2(0,0) \\ \alpha - r_1(0,0) & d + \alpha - r_1(0,0) \end{pmatrix},$$

where

$$\begin{aligned} \det(V) &= [d + \alpha - r_1(0,0)][m + r_2(0,0)] - r_2(0,0)[\alpha - r_1(0,0)] \\ &= d[m + r_2(0,0)] + m[\alpha - r_1(0,0)] > 0. \end{aligned}$$

The basic reproduction number [12,13] is defined as the spectral radius of the next generation matrix BV^{-1} , written as follows:

$$R_0 = \rho(BV^{-1}) = \frac{b_1(0,0)[m + r_2(0,0)] + b_2(0,0)[\alpha - r_1(0,0)]}{d[m + r_2(0,0)] + m[\alpha - r_1(0,0)]}. \quad (5)$$

To interpret the biological meaning of the basic reproduction number, we shall define the effective transition rate from hive bees to forager bees as follows:

$$H2F = [\alpha - r_1(0,0)] \cdot \frac{m}{m + r_2(0,0)}.$$

Recall that d is the death rate of the hive bees. The average life span of hive bees is calculated as follows:

$$LSH = \frac{1}{d + H2F}.$$

For each hive bee, during its lifespan, the average number of new hive bees produced in the next generation is calculated as follows:

$$LSH \cdot b_1(0,0) + LSH \cdot H2F \cdot LSF \cdot b_2(0,0),$$

where $LSF = 1/m$ is the average lifespan of forager bees. A simple calculation shows that the above quantity is the same as R_0 defined in (5).

2.3. Stability of Trivial Equilibrium

Theorem 1. Assume (C1)–(C2). Let R_0 be defined as in (5). The trivial equilibrium $E_0 = (0,0)$ of system (1) and (2) is locally asymptotically stable if $R_0 < 1$ and unstable if $R_0 > 1$.

Proof. The determinant of A in (3) can be calculated as follows:

$$\begin{aligned} \det(A) &= [d + \alpha - r_1(0,0) - b_1(0,0)][m + r_2(0,0)] - [\alpha - r_1(0,0)][b_2(0,0) + r_2(0,0)] \\ &= [d - b_1(0,0)][m + r_2(0,0)] + [m - b_2(0,0)][\alpha - r_1(0,0)]. \end{aligned}$$

If $R_0 < 1$, then $\det(A) > 0$. Moreover, since $m + r_2(0,0) > 0$, $\alpha - r_1(0,0) > 0$, and $b_2(0,0) + r_2(0,0) \geq 0$, we have $d + \alpha - r_1(0,0) - b_1(0,0) > 0$, and hence the trace of A is negative. Therefore, both eigenvalues of A have negative real parts. This implies local asymptotic stability of E_0 .

On the other hand, if $R_0 > 1$, then $\det(A) < 0$ and A possesses a positive eigenvalue. Thus, the trivial equilibrium E_0 is unstable. $\square$

Theorem 2. Assume (C1)–(C2). Let R_0 be defined as in (5). If $R_0 = 1$, then the trivial equilibrium $E_0 = (0, 0)$ of system (1) and (2) is locally asymptotically stable if $\eta < 0$ and unstable if $\eta > 0$, where the following is calculated:

$$\eta = \sum_{j=1}^2 \sum_{k=1}^2 \{[m + r_2(0, 0)]b_{jk}(0, 0) + [m - b_2(0, 0)]r_{jk}(0, 0)\}w_j w_k \quad (6)$$

with $w_1 = m + r_2(0, 0)$ and $w_2 = \alpha - r_1(0, 0)$.

Proof. Since $R_0 = 1$, we have $\det(A) = 0$. Moreover, 0 is a simple eigenvalue of A with a positive left eigenvector, written as follows:

$$v = \begin{pmatrix} m + r_2(0, 0) \\ b_2(0, 0) + r_2(0, 0) \end{pmatrix}$$

and a positive right eigenvector

$$w = \begin{pmatrix} m + r_2(0, 0) \\ \alpha - r_1(0, 0) \end{pmatrix}.$$

We denote the following:

$$\eta = \sum_{j=1}^2 \sum_{k=1}^2 \{[m + r_2(0, 0)][b_{jk}(0, 0) + r_{jk}(0, 0)] - [b_2(0, 0) + r_2(0, 0)]r_{jk}(0, 0)\}w_j w_k. \quad (7)$$

By Theorem 1 in [14], we obtain that E_0 is locally asymptotically stable if $\eta < 0$ and unstable if $\eta > 0$. It is easily seen that η can be simplified as in (6). This completes the proof. $\square$

2.4. Uniform Persistence

We first state a lemma that will be used frequently.

Lemma 1. Consider a matrix written as follows:

$$M = \begin{pmatrix} M_{11} & M_{12} \\ M_{21} & M_{22} \end{pmatrix} \in \mathbb{R}^{2 \times 2}.$$

- If $\det(M) < 0$, $M_{12} > 0$ and $M_{22} < 0$, then M has a positive eigenvalue $\lambda > 0$ with a positive left eigenvector (c_1, c_2) , where $c_1 = \lambda - M_{22} > 0$ and $c_2 = M_{12} > 0$.
- If $\det(M) < 0$, $M_{12} < 0$ and $M_{22} < 0$, then M has a positive eigenvalue $\lambda > 0$ with a left eigenvector $(c_1, -c_2)$, where $c_1 = \lambda - M_{22} > 0$ and $c_2 = -M_{12} > 0$.
- If $\det(M) \geq 0$, $M_{12} > 0$, $M_{21} > 0$, and $M_{22} < 0$, then $M_{11} < 0$ and M has two simple eigenvalues λ_1 and λ_2 satisfying $\lambda_1 < M_{22} < \lambda_2 \leq 0$. Moreover, the left eigenvector associated with λ_2 can be chosen as (c_1, c_2) with $c_1 = \lambda_2 - M_{22} > 0$ and $c_2 = M_{12} > 0$.

Proof. (a) If $\det(M) < 0$, then the product of the two eigenvalues of M is negative, implying that one eigenvalue is positive and the other is negative. For the positive eigenvalue $\lambda > 0$, the associated left eigenvector (c_1, c_2) , up to multiplication by a non-zero constant, is determined by the equation $c_1 M_{12} + c_2 M_{22} = \lambda c_2$. We may thus choose $c_1 = \lambda - M_{22} > 0$ and $c_2 = M_{12} > 0$.

The proof of (b) is similar to that of (a).

(c) If $M_{12} > 0$, $M_{21} > 0$, $M_{22} < 0$, and $\det(M) = M_{11}M_{22} - M_{12}M_{21} > 0$, then $M_{11} < 0$. The characteristic equation $\det(\lambda I - M) = 0$ can be written as follows:

$$\lambda^2 - (M_{11} + M_{22})\lambda + (M_{11}M_{22} - M_{12}M_{21}) = 0.$$

The discriminant of the above quadratic equation is calculated as follows:

$$\Delta = (M_{11} + M_{22})^2 - 4(M_{11}M_{22} - M_{12}M_{21}) = (M_{11} - M_{22})^2 + 4M_{12}M_{21} > 0.$$

Hence, the matrix M has two real eigenvalues, written as follows:

$$\lambda_1 = \frac{M_{11} + M_{22} - \sqrt{\Delta}}{2}, \quad \lambda_2 = \frac{M_{11} + M_{22} + \sqrt{\Delta}}{2}.$$

Since $M_{12}M_{21} > 0$, we have $\sqrt{\Delta} > |M_{11} - M_{22}|$. Consequently, $\lambda_1 < M_{22} < \lambda_2$. In particular, $\lambda_1 < 0$, which together with $\lambda_1\lambda_2 = \det(M) \geq 0$ implies that $\lambda_2 \leq 0$. Let (c_1, c_2) be a left eigenvector associated with λ_2 , then up to multiplication by a non-zero constant, this eigenvector can be determined by the equation $c_1M_{12} + c_2M_{22} = \lambda_2c_2$. Finally, we choose $c_1 = \lambda_2 - M_{22} > 0$ and $c_2 = M_{12} > 0$. The proof is complete. $\square$

Theorem 3. Assume (C1)–(C2). Let R_0 be defined as in (5). If $R_0 > 1$, then the system (1) and (2) is uniformly persistent; that is, there exists a $\delta > 0$ such that the following is valid:

$$\liminf_{t \rightarrow \infty} \min\{H(t), F(t)\} > \delta$$

for any solution with positive initial values.

Proof. We denote $X = \mathbb{R}_+^2$ and $\partial X = X \setminus X_0$, where the following is valid:

$$X_0 = \{v = (v_1, v_2) \in \mathbb{R}_+^2 : v_1 > 0, v_2 > 0\}. \quad (8)$$

It is easily seen that the maximal compact invariant set in ∂X is a singleton $\{E_0\}$, where $E_0 = (0, 0)$ is the trivial equilibrium. Given $v = (v_1, v_2) \in X$, we define the distance function as follows:

$$p(v) = d(v, \partial X) = \min\{v_1, v_2\}.$$

We claim that stable set $W^s(E_0)$ does not intersect $p^{-1}(0, \infty) = X_0$. Otherwise, there exists a solution $(H(t), F(t)) \in X_0$ for all $t \geq 0$ with the following:

$$\lim_{t \rightarrow \infty} H(t) = 0, \quad \lim_{t \rightarrow \infty} F(t) = 0.$$

For any $\varepsilon > 0$, by (C1)–(C2), there exists $t_1 > 0$ such that the following is calculated:

$$b(H(t), F(t)) \geq [b_1(0, 0) - \varepsilon]H(t) + [b_2(0, 0) - \varepsilon]F(t),$$

and

$$[r_1(0, 0) - \varepsilon]H(t) + [r_2(0, 0) - \varepsilon]F(t) \leq r(H(t), F(t)) \leq [r_1(0, 0) + \varepsilon]H(t) + [r_2(0, 0) + \varepsilon]F(t)$$

for all $t \geq t_1$.

We will consider two cases, depending on whether $b_2(0,0) + r_2(0,0)$ is positive or zero. If $b_2(0,0) + r_2(0,0) > 0$, we obtain the following from (1) and (2):

$$\begin{pmatrix} H'(t) \\ F'(t) \end{pmatrix} \geq (A - \varepsilon J) \begin{pmatrix} H(t) \\ F(t) \end{pmatrix}$$

for $t \geq t_1$, where A is given in (3) and

$$J = \begin{pmatrix} 2 & 2 \\ 1 & 1 \end{pmatrix}.$$

Note that $R_0 > 1$. It follows from a similar argument as in the proof of Theorem 1 that $\det(A) < 0$. Choose $\varepsilon > 0$ sufficiently small such that $\varepsilon < \alpha$, $2\varepsilon < b_2(0,0) + r_2(0,0)$, and $\det(A - \varepsilon J) < 0$. Since

$$(A - \varepsilon J)_{12} = b_2(0,0) + r_2(0,0) - 2\varepsilon > 0$$

and

$$(A - \varepsilon J)_{22} = -m - r_2(0,0) - \varepsilon < 0,$$

we obtain from Lemma 1 (a) that the matrix $A - \varepsilon J$ has a positive eigenvalue $\lambda > 0$ with a positive left eigenvector (c_1, c_2) . Define $u(t) := c_1 H(t) + c_2 F(t)$. We have the following:

$$u'(t) = \begin{pmatrix} c_1 & c_2 \end{pmatrix} \begin{pmatrix} H'(t) \\ F'(t) \end{pmatrix} \geq \lambda \begin{pmatrix} c_1 & c_2 \end{pmatrix} \begin{pmatrix} H(t) \\ F(t) \end{pmatrix} = \lambda u(t)$$

for $t \geq t_1$. This implies $u(t) \geq e^{\lambda(t-t_1)} u(t_1)$, which contradicts the fact that $u(t) = c_1 H(t) + c_2 F(t) \rightarrow 0$ as $t \rightarrow \infty$.

If $b_2(0,0) + r_2(0,0) = 0$, then the matrix A in (3) is lower triangular with $A_{12} = 0$. Since $R_0 > 1$, we again have $\det(A) < 0$, which together with $A_{22} = -m - r_2(0,0) < 0$ implies that

$$A_{11} = b_1(0,0) - (d + \alpha) + r_1(0,0) > 0.$$

For $t \geq t_1$, it follows from (1) and (2) that the following are valid:

$$\begin{aligned} H'(t) &\geq (A_{11} - 2\varepsilon)H(t) - 2\varepsilon F(t), \\ F'(t) &\leq [\alpha - r_1(0,0) + \varepsilon]H(t) - [m + r_2(0,0) - \varepsilon]F(t), \end{aligned}$$

where $\varepsilon > 0$ can be arbitrarily small and t_1 depends on ε . Since $A_{11} > 0$ and $\det(A) < 0$, for sufficiently small $\varepsilon > 0$ with $\varepsilon < m$ and $2\varepsilon < A_{11}$, the determinant of the perturbed matrix

$$A_\varepsilon := \begin{pmatrix} (A_{11} - 2\varepsilon) & -2\varepsilon \\ \alpha - r_1(0,0) + \varepsilon & -[m + r_2(0,0) - \varepsilon] \end{pmatrix}$$

is still negative. In view of Lemma 1 (b), A_ε has a positive eigenvalue $\lambda > 0$ with a left eigenvector $(c_1, -c_2)$, where $c_1 > 0$ and $c_2 > 0$. Define $u(t) := c_1 H(t) - c_2 F(t)$. It is clear that $u(t) \rightarrow 0$ as $t \rightarrow \infty$. On the other hand, we have the following:

$$u'(t) = c_1 H'(t) - c_2 F'(t) \geq \lambda c_1 H(t) - \lambda c_2 F(t) = \lambda u(t)$$

for $t \geq t_1$, which implies

$$u(t) \geq u(t_1)e^{\lambda(t-t_1)},$$

a contradiction. Thus, we have proven the following:

$$W^s(E_0) \cap X_0 = \emptyset.$$

Let $\Phi(t) \in C(X, X)$ be the solution semiflow corresponding to system (1) and (2). Proposition 1 implies that $\Phi(t)$ is point dissipative. By Theorem 3.4.8 in [15], the solution semiflow $\Phi(t)$ possesses a global attractor. Finally, we obtain from Theorem 3 in [16] that $\Phi(t)$ is uniformly persistent; namely, there exists a $\delta > 0$ such that

$$\liminf_{t \rightarrow \infty} p(\Phi(t)v) > \delta$$

for any $v \in X_0$. This completes the proof. $\square$

2.5. Positive Equilibrium

Theorem 4. Assume (C1)–(C2). Let R_0 and X_0 be defined as in (5) and (8), respectively. If $R_0 > 1$, then the system (1) and (2) has at least one positive equilibrium. Moreover, if the positive equilibrium is unique, then it is globally attractive in X_0 . If $b(0, y) + r(0, y) > 0$ for any $y > 0$, then the unique positive equilibrium is globally attractive in $\mathbb{R}_+^2 \setminus \{E_0\}$; namely, it attracts all solutions of (1) and (2) with non-negative and nontrivial initial values.

Proof. Consider the solution semiflow $\Phi(t)$ of system (1) and (2) restricted on X_0 . It follows from Proposition 1 and Theorem 3 that $\Phi(t)$ is point dissipative and uniformly persistent. By Theorem 4.7 in [17], the semiflow $\Phi(t) : X_0 \rightarrow X_0$ has a global attractor denoted by K , and a positive equilibrium denoted by $E_1 = (H_1, F_1)$ with $H_1 > 0$ and $F_1 > 0$. In view of (C1)–(C2), $\Phi(t)$ is monotone. If E_1 is unique, then we obtain from Theorem 3.1 in [18] that E_1 is globally attractive in X_0 .

Furthermore, if $b(0, y) + r(0, y) > 0$ for any $y > 0$, then we claim that X_0 attracts $\mathbb{R}_+^2 \setminus \{E_0\}$. When the initial values are positive: $H(0) > 0$ and $F(0) > 0$, it is obvious that $(H(t), F(t)) \in X_0$ for all $t > 0$. Now, we consider the solution with $H(0) = 0$ and $F(0) > 0$. By (1), we have $H'(0) > 0$ and hence $H(t) > 0$ for all small $t > 0$. The positive invariance of X_0 implies that $(H(t), F(t)) \in X_0$ for all $t > 0$. Next, we consider the solution with $H(0) > 0$ and $F(0) = 0$. It follows from (2) and (C2) that $F'(0) > 0$. This implies that $H(t) > 0$ for all small $t > 0$. Again, by positive invariance of X_0 , we obtain $H(t) > 0$ and $F(t) > 0$ for all $t > 0$. Therefore, the unique equilibrium E_1 attracts all solutions of (1) and (2) with $(H(0), F(0)) \in \mathbb{R}_+^2$ and $H(0) + F(0) > 0$. This completes the proof. $\square$

3. Applications

To illustrate the applications of our main results for the general model (1) and (2), we specify the functions of eclosion and social inhibition. First, we follow [19] to choose the eclosion rate, written as follows:

$$b(x, y) = \frac{L(x + y)}{w + x + y}, \quad (9)$$

where L is the maximum eclosion of brood, which is also equivalent to the laying rate of the queen [20]. The parameter w denotes the population size at which the eclosion rate is half of its maximum value. The social inhibition rate is assumed to be calculated as follows:

$$r(x, y) = \alpha cy, \quad (10)$$

where c is the hive-to-forager ratio at which social inhibition balances the transition from hive bees to forager bees [21]; that is, $r(H, F) = \alpha H$ when $H/F = c$. Hence, we arrive at the following model system:

$$H'(t) = \frac{L[H(t) + F(t)]}{w + H(t) + F(t)} - (d + \alpha)H(t) + \alpha cF(t), \quad (11)$$

$$F'(t) = \alpha H(t) - mF(t) - \alpha cF(t). \quad (12)$$

It is clear that (C1)–(C2) are satisfied. Note the following:

$$b_1(0,0) = b_2(0,0) = \frac{L}{w}, \quad r_1(0,0) = 0, \quad r_2(0,0) = c\alpha$$

The basic reproduction number defined in (5) is calculated as follows:

$$R_0 = \frac{L(m + \alpha c + \alpha)}{w[d(m + \alpha c) + m\alpha]}. \quad (13)$$

Theorem 5. Consider system (11) and (12). Let R_0 be defined as in (13). If $R_0 \leq 1$, then the trivial equilibrium $E_0 = (0,0)$ is globally asymptotically stable (in $\mathbb{R}_+^2$). If $R_0 > 1$, then E_0 is unstable, and there exists a unique positive equilibrium $E_1 = (H_1, F_1)$ that is globally asymptotically stable in $\mathbb{R}_+^2 \setminus \{E_0\}$.

Proof. A simple calculation shows that $b_{jk}(0,0) < 0$ and $r_{jk}(0,0) = 0$ for $j = 1, 2$ and $k = 1, 2$. Moreover, we note that $w_1 = m + \alpha c > 0$ and $w_2 = \alpha > 0$. Hence, the threshold parameter η defined in (6) is always negative. It then follows from Theorems 1 and 2 that the trivial equilibrium is locally asymptotically stable when $R_0 \leq 1$ and unstable when $R_0 > 1$.

Now, we assume $R_0 \leq 1$. The Jacobian matrix about the trivial equilibrium E_0 is given by the following:

$$A = \begin{pmatrix} L/w - (d + \alpha) & L/w + \alpha c \\ \alpha & -(m + \alpha c) \end{pmatrix};$$

see (3). Since $R_0 \leq 1$, we have the following:

$$\det(A) = (d + \alpha - L/w)(m + \alpha c) - \alpha(L/w + \alpha c) \geq 0.$$

Moreover, we note that $A_{12} = L/w + \alpha c > 0$, $A_{21} = \alpha > 0$, and $A_{22} = -(m + \alpha c) < 0$. Hence, it follows from Lemma 1 (c) that A possesses a nonpositive eigenvalue $\lambda \leq 0$ associated with a positive left eigenvector (c_1, c_2) such that $c_1 > 0$ and $c_2 > 0$. Let $(H(t), F(t))$ be any solution of (11) and (12) with non-negative initial values $H(0) \geq 0$, $F(0) \geq 0$, and $H(0) + F(0) > 0$. Similar as in the proof of Theorem 3, we can show that $H(t) > 0$ and $F(t) > 0$ for all $t > 0$. We then define the following:

$$u(t) := c_1 H(t) + c_2 F(t).$$

On account of (11) and (12), we have the following:

$$u'(t) = \lambda u(t) - \frac{c_1 L[H(t) + F(t)]^2}{w[w + H(t) + F(t)]}.$$

Since $\lambda \leq 0$, the function $u(t)$ is strictly decreasing in t . Note that $u(t) > 0$ for all $t > 0$. The limit is calculated as follows:

$$u_{\infty} := \lim_{t \rightarrow \infty} u(t)$$

exists and is non-negative. Now, we let $(\tilde{H}_0, \tilde{F}_0) \in \mathbb{R}_+^2$ be any limit point of the trajectory $(H(t), F(t))$; namely, there exists a time sequence t_k such that the following is calculated:

$$\lim_{k \rightarrow \infty} t_k = \infty, \quad \lim_{k \rightarrow \infty} H(t_k) = \tilde{H}_0, \quad \lim_{k \rightarrow \infty} F(t_k) = \tilde{F}_0.$$

Denote by $(\tilde{H}(t), \tilde{F}(t))$ the solution of (11) and (12) with initial values $\tilde{H}(0) = \tilde{H}_0$ and $\tilde{F}(0) = \tilde{F}_0$. By continuous dependence of solutions on the initial values, we have the following:

$$\lim_{k \rightarrow \infty} H(t + t_k) = \tilde{H}(t), \quad \lim_{k \rightarrow \infty} F(t + t_k) = \tilde{F}(t), \quad t \geq 0.$$

We define the following:

$$\tilde{u}(t) := c_1 \tilde{H}(t) + c_2 \tilde{F}(t).$$

The following is readily seen:

$$\tilde{u}(t) = \lim_{k \rightarrow \infty} u(t + t_k) = u_{\infty}.$$

This implies the following:

$$0 = \tilde{u}'(t) = \lambda \tilde{u}(t) - \frac{c_1 L [\tilde{H}(t) + \tilde{F}(t)]^2}{w[w + \tilde{H}(t) + \tilde{F}(t)]}.$$

Therefore, $\tilde{H}(t) = \tilde{F}(t) = 0$ for all $t \geq 0$. In particular, $\tilde{H}_0 = \tilde{F}_0 = 0$; namely, E_0 is the only limit point of the trajectory $(H(t), F(t))$. This proves the global attractiveness of E_0 . Together with the local asymptotic stability of E_0 , we have proved that E_0 is globally asymptotically stable (in $\mathbb{R}_+^2$).

Next, we consider the case when $R_0 > 1$. A simple calculation shows that system (11) and (12) possesses a unique positive equilibrium $E_1 = (H_1, F_1)$, where we obtain the following:

$$H_1 = \frac{w(m + \alpha c)(R_0 - 1)}{m + \alpha c + \alpha}, \quad F_1 = \frac{w\alpha(R_0 - 1)}{m + \alpha c + \alpha}.$$

The Jacobian matrix about E_1 is computed as follows:

$$J = \begin{pmatrix} l - d - \alpha & l + \alpha c \\ \alpha & -m - \alpha c \end{pmatrix},$$

where

$$l := \frac{Lw}{(w + H_1 + F_1)^2} = \frac{L}{wR_0^2} < \frac{L}{w}.$$

In view of (13) and $R_0 > 1$, we have the following:

$$\frac{L}{w} < \frac{d(m + \alpha c) + m\alpha}{m + \alpha c + \alpha}.$$

Coupling the above two inequalities gives $l < d + \alpha$ and the following:

$$(d + \alpha - l)(m + \alpha c) > \alpha(l + \alpha c).$$

Hence, the Jacobian matrix J has a negative trace and a positive determinant. The positive equilibrium E_1 is locally asymptotically stable. Theorem 4 implies that E_1 is globally attractive in $\mathbb{R}_+^2 \setminus \{(0,0)\}$. Therefore, E_1 is globally asymptotically stable in $\mathbb{R}_+^2 \setminus \{E_0\}$. This completes the proof. $\square$

The results in Theorem 5 are illustrated in Figures 1 and 2. In Figure 1, the model parameters are chosen as $L = 2000$, $w = 27000$, $\alpha = 0.25$, $m = 0.2$, $c = 0.5$, and $d = 0.01$. From (13), it is easily calculated that $R_0 \approx 0.8$. By Theorem 5, the trivial equilibrium $E_0 = (0,0)$ is globally asymptotically stable in $\mathbb{R}_+^2$.

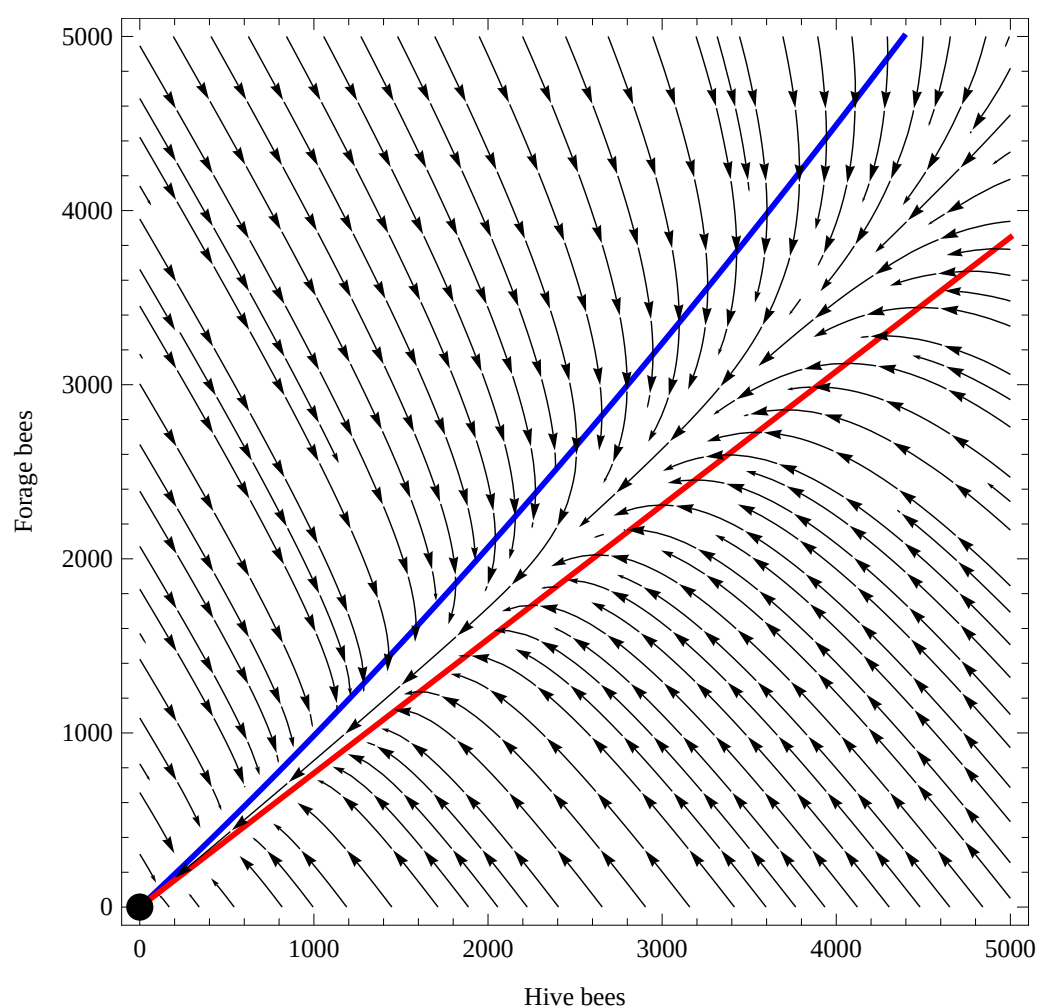


Figure 1. Phase portrait of system (11) and (12). The background arrows represent the vector field, indicating the direction of the (H, F) trajectories. The blue curve corresponds to the H -nullcline ($H' = 0$), and the red curve corresponds to the F -nullcline ($F' = 0$). Intersections of the nullclines (solid dots) indicate the equilibrium points of the system. The model parameters are chosen as $L = 2000$, $w = 27000$, $\alpha = 0.25$, $m = 0.2$, $c = 0.5$, $d = 0.01$.

In Figure 2, the parameters are set to $L = 2000$, $w = 27000$, $\alpha = 0.25$, $m = 0.1$, $c = 0.5$, and $d = 0.01$. Note that the death rate of forager bees is smaller in this second parameter set compared to the first. Using (13), we find $R_0 \approx 1.3$. According to Theorem 5, the trivial equilibrium E_0 is unstable, and there exists a unique positive equilibrium $E_1 = (H_1, F_1)$, which is globally asymptotically stable in $\mathbb{R}_+^2 \setminus \{E_0\}$. Numerical computation yields $H_1 \approx 3724$ and $F_1 \approx 4138$.

From the explicit expression in (13), it is clear that R_0 increases with L and decreases with both w and d . This behavior is biologically reasonable: a larger L or smaller w corresponds to a higher eclosion rate (see (9)), making colony persistence more likely.

Conversely, a high death rate of hive bees, d , increases the risk of colony collapse. The influence of the parameters m , α , and c on R_0 is stated in the following proposition.

Proposition 2. *The basic reproduction number R_0 defined in (13) is an increasing function of the parameter L and a decreasing function of both parameters w and d . Furthermore, we have the following sensitivity results.*

- If $m > d$, then R_0 decreases with α . If $m < d$, then R_0 increases with α . If $m = d$, then R_0 is independent of α .
- If $m > d$, then R_0 increases with c . If $m < d$, then R_0 decreases with c . If $m = d$, then R_0 is independent of c .
- As m increases, R_0 decreases.
- Denote $\beta = \alpha c$. If $m > d$, then R_0 increases with β . If $m < d$, then R_0 decreases with β . If $m = d$, then R_0 is independent of β .

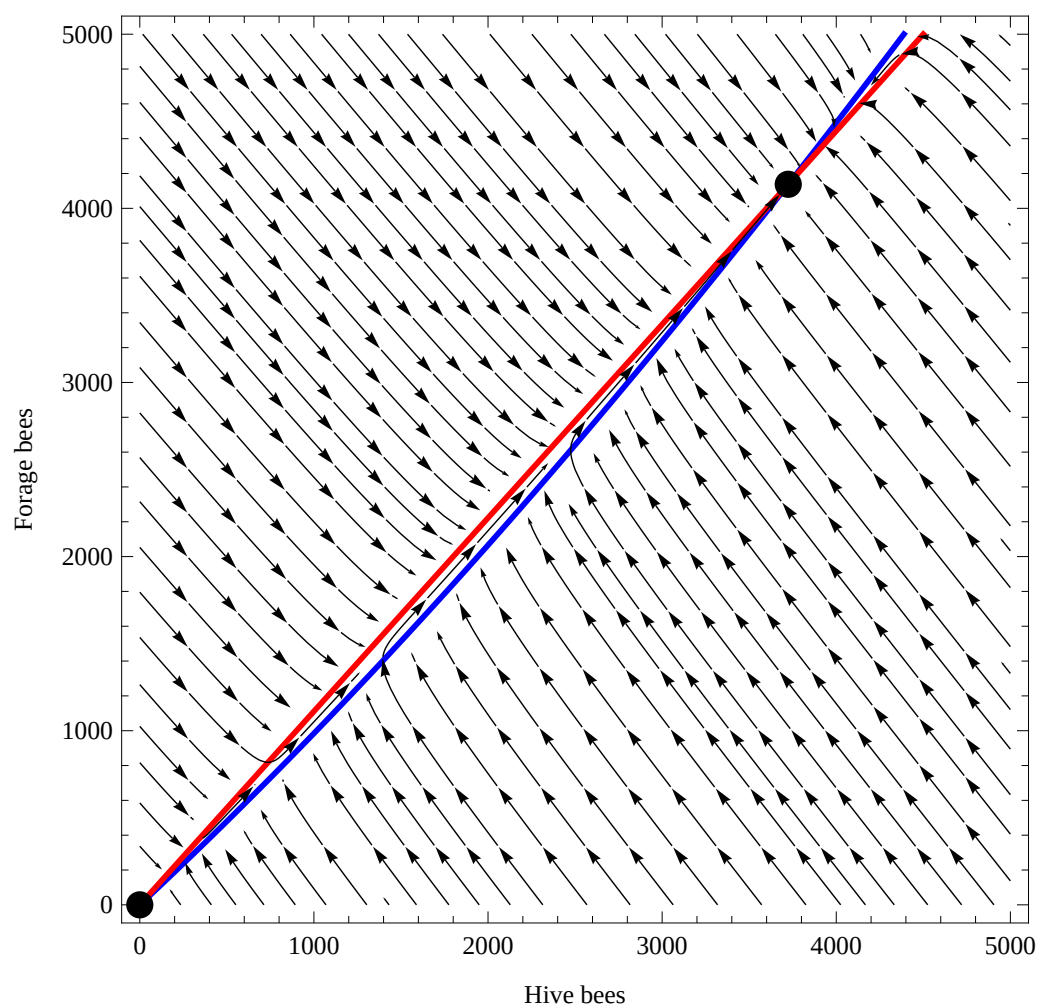


Figure 2. Phase portrait of system (11) and (12). The background arrows represent the vector field, indicating the direction of the (H, F) trajectories. The blue curve corresponds to the H -nullcline ($H' = 0$), and the red curve corresponds to the F -nullcline ($F' = 0$). Intersections of the nullclines (solid dots) indicate the equilibrium points of the system. The model parameters are chosen as $L = 2000$, $w = 27000$, $\alpha = 0.25$, $m = 0.1$, $c = 0.5$, $d = 0.01$.

Proof. (a) Note from (13) that the following is obtained:

$$\frac{w(dc + m)}{L(c + 1)} R_0 = \frac{\alpha + m/(c + 1)}{\alpha + dm/(dc + m)} = 1 + \frac{m/(c + 1) - dm/(dc + m)}{\alpha + dm/(dc + m)}.$$

Since the following is valid:

$$\frac{m}{c+1} - \frac{dm}{dc+m} = \frac{m(m-d)}{(c+1)(dc+m)},$$

we obtain

$$\frac{w(dc+m)}{L(c+1)} \frac{\partial R_0}{\partial \alpha} = \frac{m(d-m)}{(c+1)(dc+m)[\alpha + dm/(dc+m)]^2}.$$

Hence, the partial derivative $\partial R_0/\partial \alpha$ has the same sign as $d-m$. This proves (a).

(b) Similar as in the proof of (a), we rewrite (13) as follows:

$$\frac{wdR_0}{L} = \frac{c + (m+\alpha)/\alpha}{c + (dm+m\alpha)/(d\alpha)} = 1 + \frac{(m+\alpha)/\alpha - (dm+m\alpha)/(d\alpha)}{c + (dm+m\alpha)/(d\alpha)}.$$

On account of the following:

$$\frac{m+\alpha}{\alpha} - \frac{dm+m\alpha}{d\alpha} = 1 - \frac{m}{d} = \frac{d-m}{d},$$

we obtain (b).

(c) We again make use of (13) and obtain the following:

$$\frac{w(d+\alpha)R_0}{L} = \frac{m+\alpha c+\alpha}{m+d\alpha c/(d+\alpha)}.$$

Note that the following is obtained:

$$\frac{d\alpha c}{d+\alpha} < \alpha c < \alpha c + \alpha.$$

It is readily seen that R_0 is a decreasing function of m .

(d) Denote $\beta = \alpha c$. It follows from (13) that the following is valid:

$$\frac{wdR_0}{L} = \frac{\beta + m + \alpha}{\beta + m + m\alpha/d} = 1 + \frac{\alpha(1-m/d)}{\beta + m + m\alpha/d}.$$

Thus, the partial derivative $\partial R_0/\partial \beta$ has the same sign as $m-d$. This proves (d). $\square$

The biological interpretation of Proposition 2 is as follows. The mortalities of hive bees and forager bees (i.e., d and m , respectively) negatively affect R_0 . If $m < d$, meaning the death rate of forager bees is lower than that of hive bees, colony survival is promoted by a low hive-to-forager ratio c , together with a high hive-to-forager transition rate α and a low social inhibition rate αc . Conversely, if the death rate of forager bees exceeds that of hive bees ($m > d$), stronger social inhibition, combined with a low transition rate α and a high hive-to-forager ratio c , is more beneficial for the colony.

4. Conclusions

In this paper, we propose a general two-compartmental model to investigate the threshold dynamics of honey bee colonies. We explicitly derive the basic reproduction number R_0 as a critical threshold parameter, expressed in terms of the model parameters, and provide its biological interpretation. If $R_0 < 1$, then the trivial equilibrium $E_0 = (0, 0)$ is locally asymptotically stable. If $R_0 > 1$, then E_0 becomes unstable and the honey bee colony will persist. For the critical case $R_0 = 1$, we make use of a general result in [14] and find the stability conditions for E_0 . Applications of our general results are demonstrated on a specific model incorporating commonly used functions for eclosion and social inhibition. We establish the global threshold dynamics for this system: the trivial equilibrium E_0 is

globally asymptotically stable when $R_0 \leq 1$, while the unique positive equilibrium is globally asymptotically stable when $R_0 > 1$. A sensitivity analysis is performed to examine how the basic reproduction number is influenced by the model parameters, including the eclosion rate, the death rates of hive and forager bees, the social inhibition rate, and the hive-to-forager ratio.

5. Discussion

Our work has some limitations. The model we considered is monotone, and its dynamics are independent of the initial colony size. However, incorporating the Allee effect into the model [22] can lead to more complex behaviors, such as bistability. Our model includes only two compartments—hive bees and forager bees—while a more realistic approach would also account for brood dynamics [7]. In future work, we plan to investigate an age-structured model of honey bee colonies incorporating the Allee effect and the parasitic varroa mites [23]. In such a case, the trivial equilibrium should be unstable because a colony must maintain an adequate population of worker bees to provide brood care, thereby ensuring the sustained production of new individuals [24]. The maturation period of brood may play a crucial role in colony dynamics, potentially inducing Hopf bifurcations, and limit cycles. Seasonality plays a critical role in determining whether a colony persists or collapses. For instance, during winter, eclosion is greatly reduced and foraging activity ceases. Consequently, a switching periodic system offers a more realistic and meaningful framework than the autonomous system analyzed in this study. In addition, colonies in commercial beekeeping operations are often relocated. In forthcoming work, we intend to extend our analysis to a more general system that incorporates both periodicity and spatial movement. The model presented in this paper is deterministic, but it would be valuable to further investigate stochastic effects by incorporating random fluctuations in population size. While certain parameter regimes do not lead to colony collapse under the deterministic framework, the inclusion of stochasticity may change this outcome [25]. A natural extension of this study is to employ stochastic differential equations to capture vulnerabilities in colony survival that cannot be described by purely deterministic models.

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