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A Numerical Parameter Reconstruction in a Model of a Honey Bee Population

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Abstract. The model is a system of two nonlinear ordinary differential equations (ODEs) with dependent variables: the number of bees working in the hive and the number of bees that work outside the hive referred here as foragers. The population dynamics is studied. In this small study we present an effective simple algorithm to solve the parameter identification problem of the model in [10]. The parameters are identified using a least square method combined with backward Euler approximation of the ODE system and a Newton method technique for optimization of the cost functional. Numerical results of the parameters, representing the solution to the inverse problem are provided.

INTRODUCTION

Modern agriculture is increasingly reliant on managed honey bee colonies to provide a pollination service for several key horticultural crops. As a consequence, there is some concern that declining bee populations will impact horticultural productivity as well as the obvious consequences on the honey industry, see e. g. [3, 4, 9, 19, 20]. This problem has highlighted the need to better understand the factors that determine a colony's population dynamics and how they might interact with each other to understand not only why colonies sometimes fail, but also how to best manage the bee lives for optimal population growth and honey production.

Life span and mortality of the workers in honeybee colony are also influenced by the dynamic interactions between the workers in the colony. The colony typically operates as a clean, hygienic, well-provisioned and well-defined fortress, and consequently the mortality rate of the bees working exclusively within the colony in very low, see e. g. [20]. By contrast, foraging exposes bees to high level of metabolic stress and oxidative damage as well as significant risk of predation, adverse weather and getting lost. Forage mortality rates are very high: even in a strong and healthy colony forager mortality exceeds 15% per day, [9, 20]. The bee's total lifespan is, therefore, influenced by the age at which it commences foraging, and this factor is determined by mechanisms of social feedback within the colony. The age at which a bee becomes a forager is governed by pheromone-mediated systems of social inhibition.

A mathematical model allows us to explore the effects of different factors and forces on the population of the hive in a quantitative way. Such a model has the potential to make predictions about the outcome of various manipulations, and to allow a preliminary exploration of the problem before investing in experimental work. Mathematical models are capable of describing real world problems in a quantitative manner and they enable us to derive conclusions about the effects of the parameters of the system. Dynamics of a honeybee colony population have been modeled under different assumptions / constraints and the models have been used to find out the main factors of colony losses. Russel et. al. have constructed a model to link demographic dynamics of a colony to dynamics of infections and deceases within / outside the hive [15]. A more general model has been set up in terms of uninfected hive / forage bees, infected hive bees, virusfree mites and virus-infected mites in [14]. In the study [15], the factors influencing the colony failure have been analyzed and it has been determined that the breakdown of food availability and social inhibition are the main sources of colony collapse.

Applications of Mathematics in Engineering and Economics (AMEE'20) AIP Conf. Proc. 2333, 090009-1–090009-8; https://doi.org/10.1063/5.0041791 Published by AIP Publishing. 978-0-7354-4077-7/\$30.00 We are following the coupled system of ODEs models to investigate the honey bee colony population dynamics proposed by Khoury et. al. [10]. The model predicts a critical threshold forager death rate beneath which colony regulate a stable population size. If the death rates are sustained higher that this threshold, a rapid population decline is predicted and the colony failure is inevitable.

Experimental data has been used as a basis to develop and verify complex models [4, 7, 10, 13–15, 17, 20, 21] that can account for the specific conditions the studies delineate. This paper proposes an algorithm for parameter identification in the model of [10]. The fitted procedure is carried out as follows. We construct a numerical model of the honey bee colony population describing the dynamics of the number of bees working in the hive and the number of bees that work outside the hive.

The efficiency of the numerical model is crucial both from an accuracy and a speed point of view, because we set the four of the unknowns in such a way that the numerical solution obtained by the model of [10] is as close as possible to the measurements. These includes the implementation of the Gauss–Newton method [6] after the finite difference approximation of the differential equations.

In contrast, in the paper [2] of this volume, the following method is developed. There we first do quasilinearization of the differential problem and then perform the minimization of the quadratic function, which expresses the difference between the computed and measured number of bees working in and outside the hive. Comparison of these two parameter techniques is discussed in the conclusion of the present paper.

The next section introduces the model. The inverse problem is formulated in Section 3 and in Sections 4 and 5, respectively, the numerical methods for the direct and inverse problems are developed, while in Section 6 numerical simulations with synthetic and real data are presented. Conclusions are drawn in the last section.

ODE MODEL OF THE HONEY BEE POPULATION

A rapid decrease in the number of honeybee colonies has been observed since 2006 in North America [9]. The syndrome, which is characterized by the disappearance of adult bees while the limited brood and honey bees remain in the hive is known as Colony Collapse Disorder (CCD). It was first diagnosed in USA.

A detailed review of mathematical models describing bee population dynamics was presented by Becher et. al. [4], who analyzed 31 models, classified as colony, varroa, and foraging models. In [7] a simple compartment model for the worker bee population of the hive is constructed. It only considers the population of the female workers since moles (drones) do not contribute to the colony work. Let *H* be *the number of bees working in the hive* and F - the number of bees who work outside the hive hereafter referred to as*foragers*. We assume that all adult worker bees can be classified either as hive bees or as foragers, and that there is no overlap between these two behavioural classes [4, 10]. Hence the total number of adult worker bees in the colony is <math>N = H + F.

The model in [10] does not consider the impact of brood diseases on colony failure. However, it is still useful because many cases of colony failure and the extreme cases known as CCD are not caused by brood diseases [7, 20]. We assume the death rate of the hive bees is negligible. Workers are recruited to the forager class from the hive bee class and die at rate m. Let t be the time measured in days. Then, the authors of [10] represent this process with the following differential equation model:

Rate of change in hive bee numbers:

$$\frac{\mathrm{d}H}{\mathrm{d}t} = E(H,F) - HR(H,F),\tag{1}$$

eclosion recruitment to the forager class;

Rate of change in the forager numbers:

$$\frac{\mathrm{d}F}{\mathrm{d}t} = HR(H,F) - mF,\tag{2}$$

recruitment death.

The function E(H,F) describes the way eclosion depends on the number of hive bees and foragers. The recruitment rate function R(H,F) models the effect of social inhibition on the recruitment rate. It is assumed that the maximal rate of eclosion is equivalent to the queen's laying rate L and that eclosion rate approaches its maximum as N (the total number of workers in the hive) increases. In the absence of other information, we use the simplest function that increases from 0 for no workers and tends to L as N becomes very large:

$$E(H,F) = L\frac{N}{w+N} = L\frac{H+F}{w+H+F}.$$
(3)

Here w determines the rate of which E(H,F) approaches L as N gets large. Figure 2 in [10] shows E(H,F) as a function of N for a range of values of w.

We write the recruitment function as

$$R(H,F) = \alpha - \sigma \frac{F}{H+F}.$$
(4)

The first term α represents the maximal rate at which hive bees becomes foragers when there are no foragers present in the colony. The second term $-\sigma^F/H+F$ represents the *social inhibition* and, in particular, how the presence of foragers reduces the rate of recruitment of hive bees to foragers.

INVERSE PROBLEM

Following the honey bee population modeling practice, the parameters m, α , σ and w should be evaluated and their appropriate values ought to be used in the model.

We rewrite the problem (1)-(4) in the form:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = L\frac{N}{w+N} - mF,\tag{5}$$

$$\frac{\mathrm{d}F}{\mathrm{d}t} = \alpha N - (\alpha + \sigma + m)F + \sigma \frac{F^2}{N},\tag{6}$$

$$N(t_0) = N^0, \quad F(t_0) = F^0,$$
 (7)

where $p = (p^1, p^2, p^3, p^4), p^1 := m, p^2 := \alpha, p^3 := \sigma, p^4 := w$ and

$$\boldsymbol{p} \in \mathbb{S}_{\text{adm}} = \left\{ \boldsymbol{p} \in \mathbb{R}^4 : \ 0 < p^i < P^i, \ i = 1, 2, 3, 4 \right\}.$$
 (8)

Throughout this paper all solutions $\{N(t; \mathbf{p}), F(t; \mathbf{p})\}, \mathbf{p} \in \mathbb{S}_{adm}$ are defined on the interval $t_0 \leq t \leq T$. When the parameters m, α, σ and w are known, the problem (5)-(8) is well-posed and it is called a *direct problem*.

Let us assume that the coefficients m, α , σ and w are unknown. We study the *inverse problem* of identifying the parameter $p \in S_{adm}$ via the observed behaviour

$$\{N(t^{i}), F(t^{i})\}, \ i = 1, \dots, I_{\text{obs}}; \ t_{0} = t^{1} < \dots < t^{I_{\text{obs}}} = T$$

$$\tag{9}$$

of the dynamical system (5)-(8). The original problem is replaced by a minimization problem.

Then, the inverse problem of the parameter reconstruction can be formulated in a variational setting as follows:

$$\min_{\boldsymbol{p}\in\mathbb{S}_{adm}} \Phi(\boldsymbol{p}), \qquad \boldsymbol{p} = (p^1, p^2, p^3, p^4), \tag{10}$$

subjected to the solution of (5)-(8), where $\Phi(\mathbf{p})$ is defined as

$$\Phi(\boldsymbol{p}) = \frac{1}{2} \sum_{i=1}^{I_{\text{obs}}} \left[\left(N(t^i; \boldsymbol{p}) - N_{\text{obs}}(t^i) \right)^2 + \left(F(t^i; \boldsymbol{p}) - F_{\text{obs}}(t^i) \right)^2 \right].$$

Here, $\{N_{obs}(t^i), F_{obs}(t^i)\}$ are experimental data (9), and $\{N(t^i; \boldsymbol{p}), F(t^i; \boldsymbol{p})\}$ is the solution to the problem (5)-(8).

The parameter admissible set S_{adm} follows the biology of the honey bee [20] as well as the conception of the concrete model [10] and experimental data.

NUMERICAL SOLUTION TO THE DIRECT PROBLEM

The solution to the mathematical problem (5)-(8) provides the possibility for one to check the validity of the individual mathematical relationships, and whether the relationships are mutually consistent. In this case, the numerical solution is the sole option.

We introduce the piecewise-uniform mesh

$$\overline{\omega}_{\tau} = \left\{ \text{for } i = 2, \dots, I_{\text{obs}} \text{ we set } t_{j}^{i} = t^{i-1} + j\tau_{i}, \ j = 1, \dots, J_{i}, \ t^{1} = t_{0}, \ t^{i} = t^{i-1} + \tau_{i}J_{i}, \ t^{I_{\text{obs}}+1} = T \right\},$$
(11)

where $\forall i = 2, ..., I_{obs} t^i$ are the time instances at which observations are taken, t_j^i , $j = 1, ..., J_i$ and τ_i are the time points and the time step corresponding to $(t^{i-1}, t^i]$ (see fig. 1 for an example).



FIGURE 1. Mesh ω_{τ} .

For the time discretization of (5)-(6) we apply implicit Euler scheme [16]. For simplicity we assume that ω_{τ} is uniform mesh and the observation times t^i , $i = 1, 2, ..., I_{obs}$ are mesh points. In this case, we have

$$\frac{N_{j+1} - N_j}{\triangle t} = L \frac{N_{j+1}}{w + N_{j+1}} - mF_{j+1},$$
(12)

$$\frac{F_{j+1} - F_j}{\Delta t} = \alpha N_{j+1} - (\alpha + \sigma + m) F_{j+1} + \sigma \frac{F_{j+1}^2}{N_{j+1}},$$
(13)

$$N_1 = N^0, \quad F_1 = F^0. \tag{14}$$

We solve the arisen system of non-linear algebraic equations (12)-(14) by Picard iterations [16]. For each j =1,..., J-1 we construct a sequence $N_{j+1}^{s+1}, F_{j+1}^{s+1}$ such that

$$N_{j+1}^{s+1} = N_j + L \triangle t \frac{N_{j+1}^s}{w + N_{j+1}^s} - m \triangle t F_{j+1}^s,$$

$$F_{j+1}^{s+1} = F_j + \alpha \triangle t N_{j+1}^{s+1} - (\alpha + \sigma + m) \triangle t F_{j+1}^s + \sigma \triangle t \frac{(F_{j+1}^s)^2}{N_{j+1}^{s+1}}.$$
(15)

Then, the algorithm for solving the direct problem is summarized as follows.

Algorithm 1

For j = 1, ..., J - 1 do

Put $\left\{N_{j+1}^0 = N_j, F_{j+1}^0 = F_j\right\}$ the initial vector, where $\left\{N_j, F_j\right\}$ is the solution vector at time t_j . Step 1.

Step 2. For $s = 0, 1, ..., s_f$ do

- build the system (15) and calculate the new solution;
- if $\max\left\{\left|N_{j+1}^{s+1}-N_{j+1}^{s}\right|, \left|F_{j+1}^{s+1}-F_{j+1}^{s}\right|\right\| < \varepsilon$, then $N_{j+1}^{s+1}, F_{j+1}^{s+1}$ is the new approximation at time t_{j+1} , else s := s+1 and go to Step 2.1.

NUMERICAL SOLUTION TO THE INVERSE PROBLEM

In this section, we describe a numerical method and its algorithmic realization for the solution to the inverse problem (5)-(10).

For solving inverse problems, in particular, for identification of systems with known structure, the quasilinearization method (QM) is a standard tool. Designed by Bellman et. al. [5], this method was later applied to different kinds of identification problems, see e. g. [1, 13] for systems biology and references therein. We are interested in application of QM in solving the parameter identification problem (5)-(10).

We seek the point $\mathbf{p} = (p^1, p^2, p^3, p^4)$ of the local minimum of the functional $\Phi(\mathbf{p})$. Assuming that \mathbf{p} is unique, then it is the solution to $\nabla \Phi(\mathbf{p}) = 0$, or equivalently, \mathbf{p} is the solution to the system of non-linear algebraic equations

$$\frac{\partial \Phi(\boldsymbol{p})}{\partial p^r} \equiv \Phi_{p^r} = 0, \qquad r = 1, 2, 3, 4.$$
(16)

Assuming that $\nabla \Phi(\mathbf{p})$ is continuously differentiable in \mathbf{p} , we apply the Newton's method. Thus if $\mathbf{p}_{(0)}$ is the initial guess of the optimal **p**, we solve

$$\boldsymbol{p}_{k+1} = \boldsymbol{p}_k - J^{-1}(\boldsymbol{p}_k) \nabla \Phi(\boldsymbol{p}), \tag{17}$$

where $J(\mathbf{p})$ is the Jacobian of the non-linear system of algebraic equations (16). For our problem $J(\mathbf{p})$ is the Hessian matrix

$$J(\boldsymbol{p}) = \frac{\partial^2 \Phi}{\partial p^r \partial p^s} \equiv \Phi_{p^r p^s}.$$
(18)

One can expect a quadratic order of convergence

$$\|\boldsymbol{p}-\boldsymbol{p}_{k+1}\| = \mathscr{O}(\|\boldsymbol{p}-\boldsymbol{p}_k\|), \qquad \|\boldsymbol{p}_{k+1}-\boldsymbol{p}_k\| \to 0.$$

Therefore, if we compute all the terms in (18) efficiently for a given value of p, we can hope to solve the original problem with very few iterations.

The first and the second derivatives $\frac{\partial \Phi}{\partial p^r}$, $\frac{\partial^2 \Phi}{\partial p^r \partial p^s}$, which are involved in the equation (17) can be computed numerically from the solution to the direct problem (12)-(14) for different choice of the parameters. For instance, for the derivatives $\frac{\partial \Phi}{\partial p^r}$, $\frac{\partial^2 \Phi}{\partial (p^r)^2}$, $\frac{\partial^2 \Phi}{\partial p^r \partial p^s}$ we have

$$\begin{array}{lll} \frac{\partial \Phi}{\partial p^{1}} &\approx & \frac{\Phi(p^{1}+\delta_{1},p^{2},p^{3},p^{4})-\Phi(p^{1}-\delta_{1},p^{2},p^{3},p^{4})}{2\delta_{1}}, \\ \frac{\partial^{2} \Phi}{\partial (p^{1})^{2}} &\approx & \frac{\Phi(p^{1}+\delta_{1},p^{2},p^{3},p^{4})-2\Phi(p^{1},p^{2},p^{3},p^{4})+\Phi(p^{1}-\delta_{1},p^{2},p^{3},p^{4})}{\delta_{1}^{2}} \\ \frac{\partial^{2} \Phi}{\partial p^{1}\partial p^{2}} &\approx & \frac{\frac{\partial \Phi}{\partial p^{1}}(p^{1},p^{2}+\delta_{2},p^{3},p^{4})-\frac{\partial \Phi}{\partial p^{1}}(p^{1},p^{2}-\delta_{2},p^{3},p^{4})}{2\delta_{2}}. \end{array}$$

Here δ_1 and δ_2 are sufficiently small numbers. The iteration process could be terminated by different criteria. For example, if the value of the functional Φ at the point p_{k+1} is small, i. e. $|\Phi(p_{k+1})| < \varepsilon$ for a given small ε or the relative error $\frac{\|\boldsymbol{p}_{k+1} - \boldsymbol{p}_k\|}{\|\boldsymbol{p}_k\|}$ is small or the norm of the gradient $\|\nabla \boldsymbol{p}_k\|$ is small.

Then, the algorithm for solving the inverse problem is summarized as follows.

Algorithm 2

Step 1. Given / choose an initial approximation $\boldsymbol{p}_{(0)}$: (k = 0).

- Step 2. For $k = 0, 1, ..., k_f$ do
 - compute $\{N(t; p_k), F(t; p_k)\}$ solving the direct problem with Algorithm 1, calculate the increment $\Delta p_k :=$ $p_{k+1} - p_k = -J^{-1}(p_k)\nabla\Phi(p)$ and find the new approximation p_{k+1} following (17); if $\|\Delta p_k\| < \varepsilon$, then $p_{k+1} \doteq p$ is the minimum of $\Phi(p)$ thus the optimal reconstructed parameter values
 - and terminate the procedure, else k = k + 1 and go to Step 2.1.

NUMERICAL SIMULATIONS AND DISCUSSION

In this section we present numerical results in order to verify the accuracy of the proposed algorithms.

First, we solve the direct problem (5)-(7) using *real world data* from [10]. Let us set L = 2000, $\alpha = 0.25$, $\sigma = 0.75$, w = 27000. We assume two types of colonies: a small honey bee colony with $N^0 = 4500$ and an average honey bee colony with $N^0 = 9000$. In both cases at the initial time t_0 there are no foragers $F^0 = 0$. Firstly we conduct our simulations up to $t_1 = 1$ year in order to see whether, when and how the colony approaches an equilibrium state. When we assume a moderate mortality rate m = 0.24, the bee colonies thrive, see fig. 2.



FIGURE 2. The number of bees in the colony for m = 0.24: $N^0 = 4500$ (left) and $N^0 = 9000$ (right)

If the mortality rate is above a certain threshold, e. g. m = 0.4, then the colonies collapse (fig. 3).



FIGURE 3. The number of bees in the colony for m = 0.40: $N^0 = 4500$ (left) and $N^0 = 9000$ (right)

Now we explore the inverse problem. We again set L = 2000 and consider an average honeybee colony with $N^0 = 9000$ and $F^0 = 0$. We are going to identify the parameter values $\mathbf{p} = (m, \alpha, \sigma, w)^\top = (0.24, 0.25, 0.75, 27000)^\top$ and consider the problem (5)-(8) on the interval $t_0 = 0$, $t_1 = 100$ days.

Firstly, we assume the measurements (9) are taken at $t^2 = 25^{\text{th}}$, $t^3 = 50^{\text{th}}$ and $t^4 = 75^{\text{th}}$ days. We test with the initial vector $\mathbf{p}_0 = (0.5, 0.5, 0.5, 50000)^{\top}$. The results could be viewed in table 1.

It is observed that the proposed algorithm recovers the values of the implied parameters in an extremely accurate way. The relative error is of order 1e - 6, and the errors in reconstructing *m* and σ are a bit higher than 1e - 6, while the errors for α and *w* are less than it.

	p 0	р	$\pmb{p}^{ ext{impl}}$	$ \boldsymbol{p}-\boldsymbol{p}^{\mathrm{impl}} \left \frac{ \boldsymbol{p}-\boldsymbol{p}^{\mathrm{impl}} }{p} \right $
<i>m</i>	0.5	0.24	0.24	5.0457e-07 2.1024e-06
$ \alpha $	0.5	0.25	0.25	1.2425e-07 4.9701e-07
σ	0.5	0.75	0.75	2.3587e-06 3.1450e-06
<i>w</i>	50000	27000	27000	0.0203 7.5080e-07

TABLE 1. Test with $I_{obs} = 3$ observations of type (9)

Next, we conduct the experiment assuming $I_{obs} = 10$ measurements, distributed equidistantly from $t^2 = 5^{th}$ day to $t^{11} = 95^{th}$ day (table 2).

	p 0	p	p ^{impl}	$ \boldsymbol{p}-\boldsymbol{p}^{\mathrm{impl}} $	$\frac{ p-p^{\mathrm{impl}} }{p}$
<i>m</i>	0.5	0.24	0.24	1.2571e-08	5.2379e-08
$ \alpha $	0.5	0.25	0.25	1.2434e-07	4.9737e-07
$\sigma \parallel$	0.5	0.75	0.75	1.6174e-06	2.1565e-06
w	50000	27000	27000	8.6102e-04	3.1890e-08

TABLE 2. Test with $I_{obs} = 10$ observations of type (9)

In case we are provided with more observations, naturally we achieve better results. The relative error is smaller for σ and it stays the same for α . The biggest error is associated with σ , which means that *the coefficient of social inhibition rate* σ *is the most difficult to recover*. The same implication is reached in [2]. This implies that the problem (5),(6) is highly insensitive with respect to that parameter. Nevertheless, all the parameters are reconstructed with satisfactory accuracy.

CONCLUSION

The inverse problem for estimating the constant coefficients of the honey bee colony population dynamics model derived in [10] is formulated and solved numerically. For the solution to the direct problem implicit finite difference approximation is implemented by Picard iterations. Then, the discrete minimization of the least square function is done by a Gauss–Newton method.

The obtained numerical results demonstrate that the model parameters and the unknown functions, namely the number of bees working in the hive and outside the hive, are accurately estimated.

The methods developed in [2] and the one in the present study have two essential differences. In [2], for the numerical treatment of the direct (forward) problem, a quasilinearization of the differential problem is performed and on this base the cost function is introduced. Then, a sensitivity technique for its minimization is implemented.

In this paper the cost functional is formulated on the base of the differential problem. Then its minimization is realized in combination with the backward Euler approximation of the direct problem and Newton optimization technique.

It is observed that the proposed algorithm of the present study recovers the values of the implied parameters in a more accurate way.

Further we plan to use other more complex models, f. i. [8, 11]. Depending on future developments of the honey bee population we may consider models addressing time-dependent coefficients models.

For strongly nonlinear optimization problem like the one in this paper, very often is used the Levenberg– Marquardt method, see e. g. [12]. It is a tricky combination of two classical optimization methods: the Newton and the gradient method. We will compare the efficiency of the Levenberg-Marquardt method with the ones we have implemented.

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