



# Comment on “An approach to the modeling of honey bee colonies” by Romero-Leiton et al. (2022)

Piotr Grabowski<sup>a,☆</sup>

<sup>a</sup>formerly at: Institute of Control Engineering and Robotics, AGH University of Science and Technology,  
Kraków, Poland  
<sup>☆</sup>retired

**Correspondence:** Piotr Grabowski (pgrab@agh.edu.pl)

Received: 21 August 2024 – Revised: 7 November 2024 – Accepted: 8 November 2024 – Published: 9 January 2025

**Abstract.** The results of a recent paper on the modeling of a honey bee colony have been supplemented and strengthened by showing that the domain of biological validity of a mathematical model with unstable singularity removed is contained in the domain of attraction of positive stable equilibrium. The results go beyond these of the commented paper.

## 1 Introduction

Due to ecological role of honey bees, it is important to more accurately assess the stability of honey bee colonies. Recently, Romero-Leiton et al. (2022) (Sect. 3) proposed a mathematical model of honey bee colony dynamics in the form of a 3-dimensional nonlinear autonomous system. The asymptotic stability analysis has been local and examined by the linearization.

Observe that their model can be decomposed into the population part:

$$\dot{B} = \beta f(T) - bB, \quad \dot{T} = \omega B - aT \quad (1)$$

and the equation of honey production  $M$  is as follows:

$$\dot{M} = \rho \frac{T}{T+u} - \alpha M - \delta T M, \quad (2)$$

which significantly facilitates an analysis. Equation (1) is classified as the age/structure model (Chen et al., 2021).

$B$  and  $T$  are populations of immature and adult honey bees, respectively;  $\beta$  stands for immature bee reproduction rate;  $\omega$  is adult bee maturation rate;  $a := \sigma + \mu_T$ , where  $\sigma$  is adult bee death rate from a stressful factor;  $\mu_T$  is adult bee natural death rate;  $b := \mu_B + \omega$ , and  $\mu_B$  denotes immature bee natural death rate. The *eclosion* function  $f$  has the form of Hille’s sigmoidal function of the first order  $f(y) = \frac{y}{y+v}$ , where  $v$  stands for an average saturate rate (number of adult

bees needed for immature bees to reach half of its maximum number). Notice that  $f$  is strictly increasing.

$M$  is honey production;  $\rho$  is honey production rate;  $\alpha$  denotes rate of honey loss due to natural causes;  $\delta$  stands for honey bee consumption rate in adult state, and  $u$  is an average saturate rate.

Positive quadrant  $\mathbb{R}^{2+}$  (octant  $\mathbb{R}^{3+}$ ) is the domain of biological validity of Eq. (1) (Eqs. 1 and 2).

The system Eq. (1) has always an equilibrium at the origin and a desired positive equilibrium  $(B_0, T_0)$ , and clearly

$$0 = \beta f(T_0) - bB_0, \quad 0 = \omega B_0 - aT_0. \quad (3)$$

The equilibrium point of Eq. (1) at zero ought to be an unstable saddle point, which is the case if and only if

$$\frac{1}{v} > \frac{ab}{\omega\beta} := k, \quad (4)$$

where  $k^{-1}$  is called *ecological threshold*. Then the one-dimensional stable eigenspace of the linearized version of Eq. (1) at  $(0, 0)$  is the supporting line of  $\mathbb{R}^{2+}$ . By *translation of coordinates*  $x_1 := B - B_0$  and  $x_2 := T - T_0$ , we reduce

Eq. (1) to

$$\dot{x}_1 = \beta g(x_2) - bx_1, \quad \dot{x}_2 = \omega x_1 - ax_2, \quad (5)$$

$$g(y) := f(y + T_0) - f(T_0) = \frac{vy}{(T_0 + v + y)(T_0 + v)}, \quad (Eq. 1.3)$$

$$g(0) = 0, \quad g(-T_0) = -\frac{T_0}{T_0 + v} \stackrel{(Eq. 1.3)}{=} -\frac{bB_0}{\beta} = -kT_0. \quad (6)$$

The translation maps  $\mathbb{R}^{2+}$ , the domain of biological validity of the model (Eq. 1), onto  $S_0 := [-B_0, \infty) \times [-T_0, \infty)$ .

## 2 Preliminary analysis

Combining Eq. (5) we establish that  $x_2$  satisfies the Liénard equation (LaSalle and Lefschetz, 1961, p. 59):

$$\ddot{x}_2 = -(a + b)\dot{x}_2 - \omega\beta[kx_2 - g(x_2)].$$

Whence the energetic Lyapunov functional (weakly decreasing along solutions)

$$V = \frac{\dot{x}_2^2}{2\omega\beta} + \int_0^{x_2} [ky - g(y)] dy, \quad \dot{V} = -\frac{a + b}{\omega\beta} \dot{x}_2^2 \leq 0$$

is readily available (LaSalle and Lefschetz, 1961, p. 60).

A set is *invariant* if solutions map this set into itself and *strongly invariant* if they map this set onto itself.

**Lemma 2.1.** The sector  $S_0$  is an invariant subset for solutions of Eq. (5).

*Proof.* With Eq. (6), on a semi-straight line ( $x_1 = -B_0, x_2 \geq -T_0$ ), it holds that

$$\dot{x}_1 = \beta g(x_2) - bx_1 \geq \beta g(-T_0) + bB_0 = -\frac{abT_0}{\omega} + b\frac{aT_0}{\omega} = 0,$$

and trajectories weakly enter  $S_0$ . Similarly on a semi-straight line ( $x_1 \geq -B_0, x_2 = -T_0$ ), one has

$$\dot{x}_2 = \omega x_1 - ax_2 \geq -\omega B_0 + aT_0 = 0,$$

so therein trajectories weakly enter  $S_0$ .

## 3 Main results

**Theorem 3.1.** Assume that Eq. (4) holds. Every solution of Eq. (5) starting from  $S_0 \setminus \{(B_0, -T_0)\}$  tends to zero.

*Proof.* Thanks to Lemma 2.1 and since  $V$  is a Lyapunov functional, for every  $l \geq 0$ , the set  $\Omega := \{x \in S_0 : V(x) \leq l\}$  is invariant and compact (closed and bounded). The *strongly invariant limit set* contained in  $\{x \in \Omega : \dot{V} = \dot{x}_2 = \omega x_1 - ax_2 = 0\}$  consists of two equilibrium points. Indeed  $\dot{x}_2 \equiv 0$  implies  $\ddot{x}_2 \equiv 0$ , which with the

Liénard equation leads to  $kx_2 \equiv g(x_2)$ . Now, with Eq. (6), either  $x_2 \equiv 0$  or  $x_2 \equiv -T_0$ . In the first case  $x_1 \equiv 0$ , and in the second one  $x_1 = -B_0$ . The second case is eliminated by excluding the unstable equilibrium point. Modifying the result slightly (LaSalle and Lefschetz, 1961, Theorem VI, p. 58) or applying directly the result of Grabowski (2020, Theorem 1.4), we get the claim.

Importing  $T = T(t)$  from Eq. (1), we can regard Eq. (2) as a linear nonautonomous equation.

$$\dot{M}(t) = -[\alpha + \delta T(t)]M + \rho \frac{T(t)}{T(t) + u}, \quad t \geq 0$$

with the solution  $M(t) = M_1(t) + M_2(t)$ , where

$$M_1(t) := \exp\left(-\int_0^t [\alpha + \delta T(\tau)] d\tau\right) M(0),$$

$$M_2(t) := \frac{\int_0^t \frac{\rho T(\tau)}{T(\tau) + u} \exp\left(\int_0^\tau [\alpha + \delta T(s)] ds\right) d\tau}{\exp\left(\int_0^t [\alpha + \delta T(s)] ds\right)}.$$

$M_1(t)$  exponentially decays to 0. With Theorem 3.1, for  $(B(0), T(0)) \in \mathbb{R}^{2+} \setminus \{0\}$ , it holds that  $T(t) \rightarrow T_0$  as  $t \rightarrow \infty$ . Then, applying L'Hôpital's rule, we get

$$\lim_{t \rightarrow \infty} M(t) = \frac{\rho T_0}{(T_0 + u)(\alpha + \delta T_0)} := M_0,$$

so  $M(t) \rightarrow M_0$  as  $t \rightarrow \infty$  and  $M(t) > 0$ , provided that  $M(0) > 0$ . It is easy to see that  $M_0$  is an equilibrium of Eq. (2). Thus, from Theorem 3.1 we obtain the following corollary.

**Theorem 3.2.** Assume that Eq. (4) holds. The domain of biological validity  $\mathbb{R}^{3+}$  of the full model (Eqs. 1 and 2) with unstable equilibrium at 0 removed is the domain of attraction of the positive equilibrium.

## 4 Conclusions

Theorem 3.2 describes the global behavior of the full system and goes beyond the results of Romero-Leiton et al. (2022, Sect. 3), which were local ones, in a neighborhood of positive equilibrium points. Basic facts are the following: (i) the original model admits a decomposition, and (ii) Eq. (1) is related to the Liénard equation for which (iii) some construction of Lyapunov functionals are known (LaSalle and Lefschetz, 1961, p. 60, p. 115 and Grabowski, 2020, Sect. 2).

Let us indicate ecological aspects of our results:

- i. The colony stability is much more robust than it would be following the linearization; i.e., larger deviations of initial conditions from the steady state are allowed (deviations of initial conditions can be interpreted as the Dirac-type impulses additively disturbing the system).
- ii. The colony reaches this via the internal stabilizing feedback realized by the eclosion.

iii. The eclosion function may have a different form than Eq. (5), provided that  $\frac{g(y)}{y} < k$  for  $y > 0$  and the line  $ky$  is not an asymptote for  $g$  (this is needed to have level sets of  $V$  bounded as required in the proof of Theorem 3.2).

**Data availability.** No data sets were used in this article.

**Competing interests.** The author has declared that there are no competing interests.

**Disclaimer.** Publisher’s note: Copernicus Publications remains neutral with regard to jurisdictional claims made in the text, published maps, institutional affiliations, or any other geographical representation in this paper. While Copernicus Publications makes every effort to include appropriate place names, the final responsibility lies with the authors.

**Acknowledgements.** The author thanks Grażyna Halastra for conversations concerning beekeeping.

**Review statement.** This paper was edited by Daniel Montesinos and reviewed by two anonymous referees.

## References

- Chen, J., DeGrandi-Hoffman, G., Ratti, V., and Kang, Y.: Review on mathematical modeling of honeybee population dynamics, *Math. Biosci. Eng.*, 8, 9606–9650, <https://doi.org/10.3934/mbe.2021471>, 2021.
- Grabowski, P.: Nonlinear Control System, [http://home.agh.edu.pl/~pgrab/grabowski\\_files/nonlinear/nonlinear.xml](http://home.agh.edu.pl/~pgrab/grabowski_files/nonlinear/nonlinear.xml) (last access: 11 December 2024), 2020.
- LaSalle, J. P. and Lefschetz, S.: *Stability by Liapunov’s Direct Method with Applications*, Ac Press, New York, 1961.
- Romero-Leiton, J. P., Gutierrez, A., Benavides, I. F., Molina, O. E., and Pulgarín, A.: An approach to the modeling of honey bee colonies, *Web Ecol.*, 22, 7–19, <https://doi.org/10.5194/we-22-7-2022>, 2022.