

Review of a Predator-Prey Model with Two Limit Cycles

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Abstract

It is well-known that the Lotka-Volterra predator-prey model has a family of periodic orbits, but does not possess limit cycles and therefore the model is said to be structurally unstable. The Lotka-Volterra model is a special case of a much larger group namely the quadratic population models and it can be shown that none of them can produce limit cycles. The surprising finding is that by combining two quadratic models a quadratic population model with two limit cycles is uncovered. Although the model looks simple at first glance it provides a rich source of dynamics and deserves attention.

In this paper we revisit a model that has its origin in the work of Dubois and Closset [1]. A set of two quadratic population models interact as piecewise defined differential equations. The model has been discussed by Ren Yongtai and Han Li [2], cryptically written and showing some linguistic and typographical errors, but providing an excellent vehicle for developing skills in mathematical modeling, differential equations and technology for the young researcher.

We explore the model in clearer detail and supplement the theory with rich graphical illustration. The paper has the purpose of providing an example of how a young researcher, such as a post graduate student in biomathematics, can expand on an existing model by making use of current technology.

KEYWORDS: Quadratic population model, biomath education, limit cycles, piecewise-defined differential equations

1. Introduction

In a previous discussion paper Van der Hoff [4] highlighted the problems encountered by biology students not having enough mathematics and vice versa. It has become apparent that no single discipline can fully address the challenges of new frontiers in biology [5], and as such the average life science student is not exposed to enough areas in mathematics [3]. It was suggested that mathematical biology students must be encouraged to work across disciplinary boundaries. Here we propose an example that students of mathematics, biology or biomathematics might find accessible. The example stems from a paper that is not only dated but somewhat flawed and difficult to follow. We first provide background.

The paper of Yongtai and Li [2] builds on the work of Dubois and Closset [1] on the time-dependent horizontal structuration of plankton populations called the patchiness effect, presented at a marine biology symposium in 1975. Interaction between phytoplankton and herbivorous zooplankton result in a predator-prey model.

In the simplified model

$$\begin{aligned}\frac{dx}{dt} &= k_1 x(1 - \alpha x) - k(x)y \\ \frac{dy}{dt} &= -k_3 y + \beta k(x)y\end{aligned}\tag{1}$$

$x(t)$ represents the phytoplankton biomass (the prey) and $y(t)$ the zooplankton biomass (the predator). The term $k(x)$ is called the grazing function. Dubois and Closset [1] present numerical simulations of the predator-prey models, varying the grazing rate. Small changes in the shape of the grazing curve lead to drastic differences in the plankton dynamics. Conditions are given for which there is (i) one stable stationary state, (ii) one stable stationary state and one stable limit cycle and (iii) one stable stationary state, one unstable limit cycle and one stable limit cycle. The third case of two limit cycles is of great importance for the explanation of patchiness initiation according to Dubois and Closset [1]. They show that if the grazing function $k(x)$ takes the form

$$k(x) = \begin{cases} k_2 x, & \text{if } x \leq \tau \\ k_2 \tau, & \text{if } x > \tau \end{cases}\tag{2}$$

then the system has two limit cycles. Here τ represents the phytoplankton concentration at which saturation occurs, so τ is a threshold under which the grazing is linear and over which the grazing is constant. Under the threshold fluctuations are damped and over the threshold fluctuations are amplified initiating the emergence of new time and space patterns.

Furthermore τ, k_1, k_2 and k_3 are positive constants while $\alpha \geq 0$ and $\beta \geq 0$. The system (1 and 2) takes on the properties of a typical Lotka-Volterra predator-prey system, where logistic growth of the prey species $x(t)$ is reflected by the $-k_1 \alpha x^2$ term.

Dubois and Closset [1] use the system (1 and 2) to describe the patchiness effect of a plankton wave which is applicable in the field of marine biology. However, since it is in essence a Lotka-Volterra system subjected to piecewise conditions the system can likely be applied to other applications displaying predator-prey interactions.

When $x \leq \tau$, the system is governed by a linear predation rate where interaction is directly proportional to the availability of prey, but when $x > \tau$, the interaction between predator and prey describes a special case of the so-called Holling Type predation pattern, where predation is determined by the relative “fullness” of the predator in combination with emigration and immigration patterns of the prey species.

Dubois and Closset [1] found evidence on computer that System (1) have two limit cycles and the paper by Yongtai and Li [2] does a qualitative analysis to confirm Dubois and Closset's [1] conclusion of their existence. The analysis of Yongtai and Li [2] is cryptically written with three theorems and three lemmas as well as their proofs condensed to fill less than two pages. The paper has evidently not been language edited and therefore makes reading and comprehension difficult. For example, in the abstract of their paper the equation

• $\dot{x} = k_1(x - \alpha x) - k(x)y$ is incorrect. Further mistakes are subsequently pointed out in our paper. An undergraduate student (or even a graduate student) in mathematics would find it near impossible to make sense of the paper. A student in biology would most likely not be able to digest the paper at all, which has its roots in marine biology.

The purpose of this paper is firstly to present the results of the Yongtai and Li [2] paper in such a way that students from both a mathematical and biological background can work through it with fair ease. Graphical representations are generously presented to further the reader's understanding.

2. Discussion

First consider the quadratic population model given by

$$\begin{aligned}\frac{dx}{dt} &= x(a_0 + a_1x + a_2y) \\ \frac{dy}{dt} &= y(b_0 + b_1x + b_2y)\end{aligned}\tag{3}$$

where a_i and b_i are real constants ($i = 0,1,2$). This model has been well investigated by amongst others: Bautin [7, 8], Coppel [9], Coleman [10] and Van der Vaart [11]. In the latter, Van der Vaart confirms that this model can never have limit cycles, and finds conditions for the equilibrium point in the population quadrant to be a center, thereby resulting in a family of closed curves.

System (1) is an example of System (3), with the difference that it is subjected to piece-wise conditions.

For $x \leq \tau$, System (1) results in a typical predator-prey system

$$\begin{aligned}\frac{dx}{dt} &= k_1x - k_1\alpha x^2 - k_2xy \\ \frac{dy}{dt} &= -k_3y + \beta k_2xy\end{aligned}\tag{A}$$

and for $x > \tau$,

$$\begin{aligned}\frac{dx}{dt} &= k_1x - k_1\alpha x^2 - k_2\tau y \\ \frac{dy}{dt} &= -k_3y + \beta k_2\tau y\end{aligned}\tag{B}$$

where the constant $\tau > 0$ acts as a prey population concentration threshold that will change the nature of the predator-prey interaction. The functions that make up System (1) are piecewise continuous and of exponential order, hence the existence and uniqueness of solutions can be confirmed [12]. Neither of the two Systems (A) or (B), considered individually, have limit cycles because they are both of the form of System (3) (Van der Vaart [11]).

System (A), with $x \leq \tau$, has three equilibrium points, namely

$$S_1 = (0;0), S_2 = \left(\frac{1}{\alpha};0\right) \text{ and } S_3 = \left(\frac{k_3}{\beta k_2}; \frac{k_1}{k_2} \left(1 - \alpha \frac{k_3}{\beta k_2}\right)\right)$$

and System (B), with $x > \tau$, has two equilibrium points, $S_1 = (0;0)$ and $S_2 = \left(\frac{1}{\alpha};0\right)$.

Note that there is a typographical error in the Yongtai and Li [2] paper in the writing of S_3 .

It should also be noted that S_3 is physically relevant if and only if $\alpha \frac{k_3}{\beta k_2} < 1$.

Equilibrium points S_1 and S_2 predict extinction of one or both species and naturally neither is surrounded by closed curves contained in the population quadrant, which is a prerequisite for the existence of a limit cycle in population models. Equilibrium point S_3 is therefore the only likely candidate as equilibrium point to be surrounded by a closed periodic trajectory.

If $\frac{k_3}{\beta k_2} \geq \tau$, for both System (A) and (B), it follows that $\frac{dy}{dt} \leq 0$ for all (x,y) in the first quadrant, and by the Bendixson negative criterion [12] no limit cycles are possible. This was stated as Theorem 1 in the Yongtai and Li [2] paper, with no reference to the Bendixson criteria which might make it more difficult to understand how they reached their conclusion of no limit cycles being possible.

So assume that $\frac{k_3}{\beta k_2} < \tau$. To further investigate the properties of

$S_3 = \left(\frac{k_3}{\beta k_2}; \frac{k_1}{k_2} \left(1 - \alpha \frac{k_3}{\beta k_2}\right)\right)$ first consider the case when $\alpha = 0$. This case was dealt with as

Lemma 2 in the Yongtai and Li [2] paper. The explanation in this paper gives more detail which can assist in understanding.

Special Case: $\alpha = 0$

System (1) now becomes

$$\begin{aligned} \frac{dx}{dt} &= k_1 x - k(x)y \\ \frac{dy}{dt} &= -k_3 y + \beta k(x)y \end{aligned} \tag{4}$$

with

$$k(x) = \begin{cases} k_2 x, & \text{if } x \leq \tau \\ k_2 \tau, & \text{if } x > \tau \end{cases}$$

simplifying, for $x \leq \tau$, to

$$\begin{aligned}\frac{dx}{dt} &= k_1 x - k_2 xy \\ \frac{dy}{dt} &= -k_3 y + \beta k_2 xy\end{aligned}\tag{A*}$$

and for $x > \tau$ to

$$\begin{aligned}\frac{dx}{dt} &= k_1 x - k_2 \tau y \\ \frac{dy}{dt} &= -k_3 y + \beta k_2 \tau y\end{aligned}\tag{B*}$$

System (A*) has two equilibrium points $S_1 = (0,0)$, which is a saddle, and $S_3^* = \left(\frac{k_3}{\beta k_2}, \frac{k_1}{k_2} \right)$

a center, lying in the interior of the first quadrant. By taking the ratio of $\frac{dy}{dt}$ to $\frac{dx}{dt}$, System (A*) is reduced to a single separable differential equation. The solutions to this system are closed periodic solutions defined by $k_1 \ln y - k_2 y + k_3 \ln x - \beta k_2 x = c$, where c is a constant of integration. Therefore S_3^* is a center surrounded by infinitely many steady states, each depending on its unique initial value (x_0, y_0) .

The solution to System (B*) is $y = \frac{k_1 + k_3 - \beta k_2 \tau}{k_2 \tau} x - c_1 \frac{e^{k_1 t} (k_1 + k_3 - \beta k_2 \tau)}{k_2 \tau}$ so for $c_1 = 0$

the system has a straight line solution, say L_1 , given by $y = \frac{k_1 + k_3 - \beta k_2 \tau}{k_2 \tau} x$ that passes

through the origin. If we assume that $k_1 + k_3 - \beta k_2 \tau > 0$ then L_1 has a positive gradient.

Now consider the combined solutions of Systems (A*) and (B*), subject to the piecewise defined conditions. When the x -values defining the trajectory become greater than τ , the trajectory will intersect the vertical line $x = \tau$, and the characteristics of System (B*) will then govern the future path of the trajectory. The vector field of System (4) is shown in Figure 1 on which the demarcation brought about by $x = \tau$ is clear.

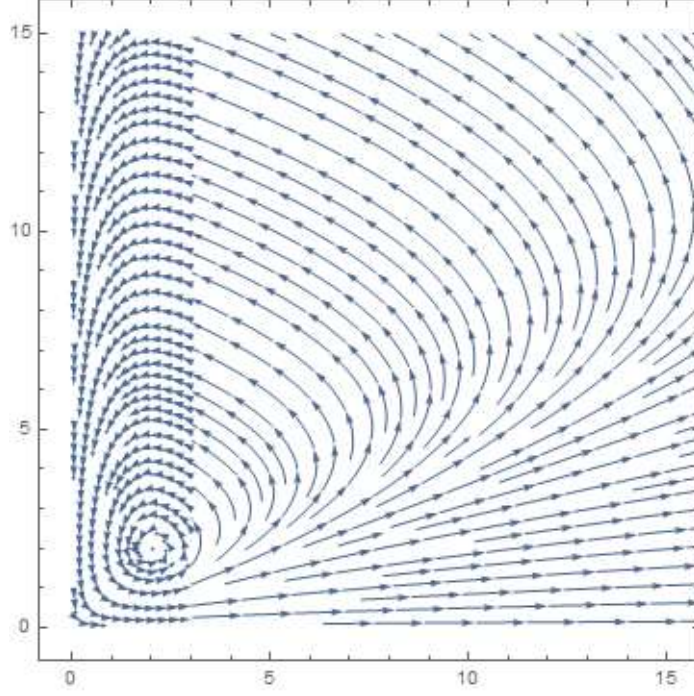


Figure 1: The vector field of System (4).

Some of the closed curve solutions of System (A*), as shown in Figure 2, must intersect the straight line $x = \tau$ in two points. We consider one of these closed curve solutions and denote the points of intersection as $P_0(\tau, y_0)$ and $P_1(\tau, y_1)$.

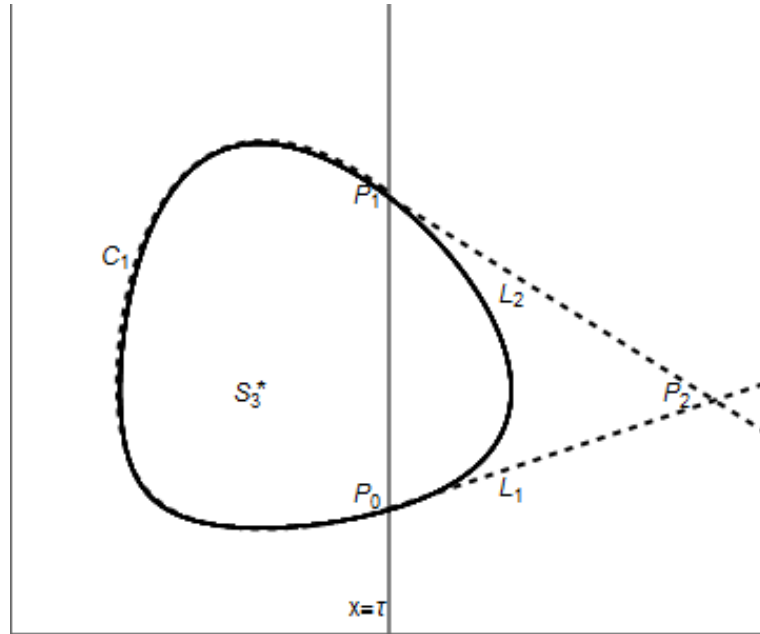


Figure 2: Closed curve intersecting $x = \tau$ in $P_0(\tau, y_0)$ and $P_1(\tau, y_1)$

We choose initial value $P_0(\tau, y_0)$ where $y_0 = \frac{k_1 + k_3 - \beta k_2 \tau}{k_2}$ so that it is situated on the straight line L_1 which is a solution to System (B*). Note that there is a typographical error in the Yongtai and Li [2] paper in the typing of y_0 .

It would therefore be possible to construct at least one straight line segment, say L_2 , with negative gradient, connecting $P_1(\tau, y_1)$ to some point on the solution L_1 of System (B*), say P_2 , for which the vector field of System (4) will depart in an upward direction as shown in Figure 3.

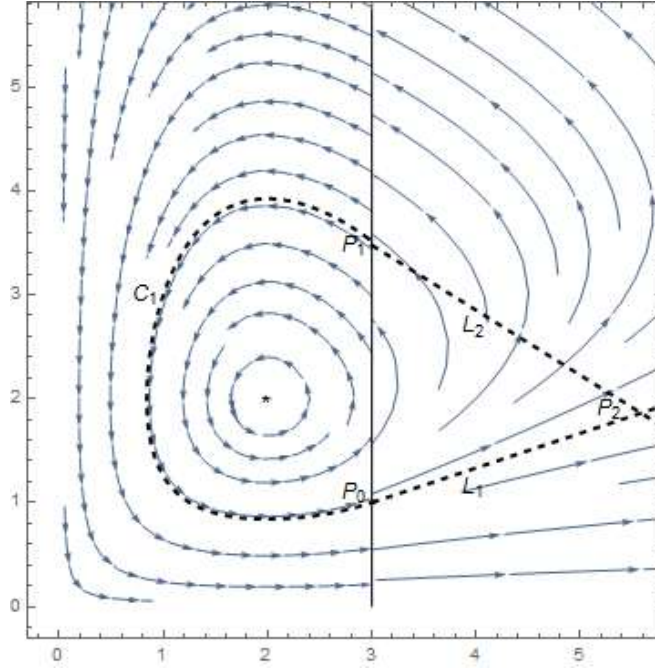


Figure 3: Vector field of System (4)

For System (4) there now exists a simple closed region defined by curve $C = \overline{P_1 P_0} \cup \overline{P_0 P_2} \cup \overline{P_2 P_1}$ where $\overline{P_1 P_0}$ is the solution curve segment C_1 of System (A*), $\overline{P_0 P_2}$ is the solution line segment L_1 of System (B*), and $\overline{P_2 P_1}$ is the straight line segment L_2 on which the vector field of System (4) departs in an upward direction. There are several mistakes in the Yongtai and Li [2] paper that makes visualization of the region difficult. This region is illustrated in Figure 4. This figure serves as a valuable illustration and was not included in the paper by Yongtai and Li [2]. The parameter values used to generate the figures are as follows: $k_1 = 2, k_2 = 1, k_3 = 2, \beta = 1$ and $\tau = 3$. So $S_3^* = (2, 2)$ is a center if $x \leq 3$ and L_1 is the straight line solution if $x > 3$.

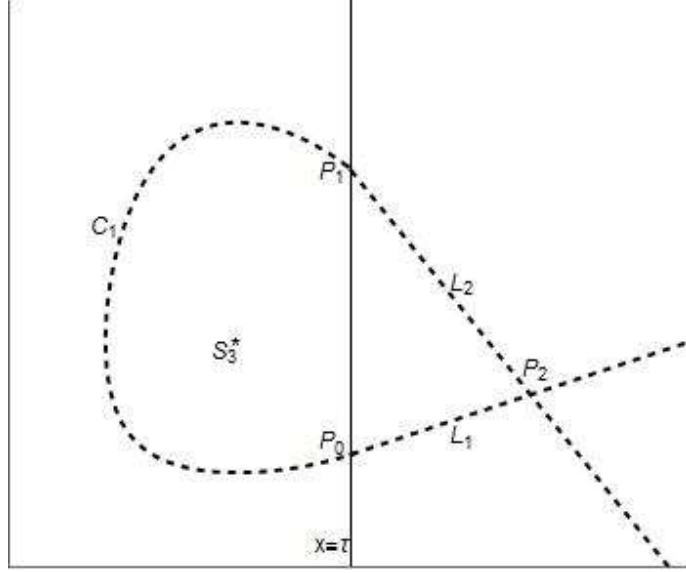


Figure 4: The curve C defined for System (4)

The region enclosed by C is such that, for System (4), there is no vector field entering the region, implicating that all solution curves generated outside this region in positive time will remain outside the region. Any solution curve initiated, in negative time, from inside the region C will be attracted by the limit cycle as is the case when initiated from outside the region C in negative time as is shown in Figure 5.

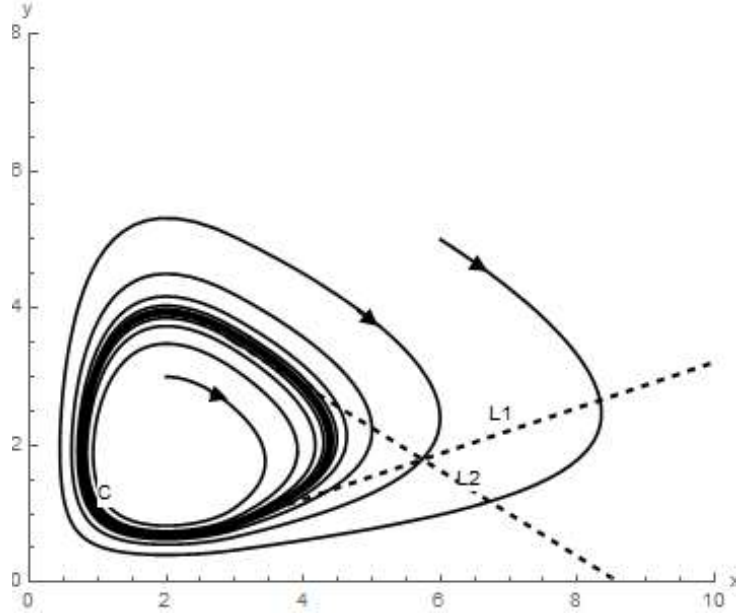


Figure 5: Solution curves attracted to the limit cycle in negative time.

Case when $0 < \alpha \ll 1$ (Theorem 2 in the Yongtai and Li [2] paper.)

By the principle of continuous dependence of solutions on parameters for $0 < \alpha \ll 1$, System (1) still has a closed curve C on which no vector field of System (1) will enter the interior.

The general continuous dependence of solutions on parameters allows us to derive qualitative

statements regarding nonlinear systems [13] as long as we stay sufficiently close to $\alpha = 0$.

Thus for $\frac{k_3}{\beta k_2} < \tau$ and $k_1 + k_3 - \beta k_2 \tau > 0$. System (1) has a limit cycle with S_3 as equilibrium point.

Furthermore, for System (1) and for some large value of h , that is $h \gg 1$, there exists a straight line, say L_3 , defined by $y + \beta x = h$ on which there is no vector field of System (1) tending upwards from it. This is motivated as follows:

Consider

$$\begin{aligned} \frac{dL_3}{dt} &= \frac{d}{dt}(y + \beta x) = \frac{dy}{dt} + \beta \frac{dx}{dt} \\ &= (-k_3 + \beta k(x))y + \beta(k_1 x(1 - \alpha x) - k(x)y). \end{aligned}$$

But $y = -\beta x + h$, therefore

$$\begin{aligned} \frac{dL_3}{dt} &= (-k_3)(h - \beta x) + \beta(k_1 x(1 - \alpha x)) \\ &= x\beta k_1 - hk_3 + x\beta k_3 - x^2\alpha\beta k_1 \\ &= -(\alpha\beta k_1 x^2 - \beta(k_1 + k_3)x + hk_3) \end{aligned}$$

Thus, for some large value of h , the gradient $\frac{dL_3}{dt} < 0$ for all (x, y) so that the vector field for

System (1) departs upwards on L_2 and anticlockwise away from L_3 . We have provided more detail than in the Yongtai and Li [2] paper presented there as Lemma 3. So we now have two regions: one inside the curve C , say R_1 and one outside the curve C but below L_3 , say R_2 . This is depicted in Figure 6.

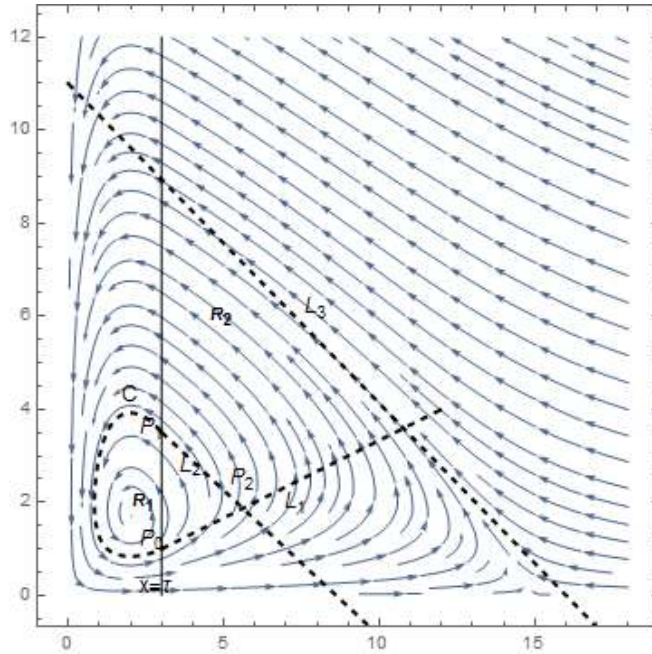


Figure 6: Vector fields of System (1) showing the regions R_1 and R_2 .

This results in a second limit cycle being formed. This result is presented in the Yongtai and Li [2] paper as Theorem 3. The illustration provided in Figure 6 should help to understand how the second limit cycle is formed.

Neither Dubois and Closset [1] or Yongtai and Li [2] included examples in their papers. We illustrate the existence of the two limit cycles by the following example.

Example

Parameter values are chosen to satisfy the conditions dealt with in this paper. It has no bearing on any specific predator-prey interactions and the novelty lies within the discovery of the two limit cycles.

Choose $k_1 = 2$; $k_2 = 1$; $k_3 = 2$; $\tau = 3$; $\beta = 1$ and $\alpha = 1/15$ so that $k_3 - \beta k_2 \tau < 0$ and $k_1 + k_3 - \beta k_2 \tau > 0$. Equilibrium point S_3 is now a stable spiral point as shown in Figure 7. All trajectories initiated in positive time from within the region R_1 spirals towards the equilibrium point S_3 (in this case $(2, \frac{26}{15})$). In negative time the trajectories will be attracted to the limit cycle as also shown in Figure 5 and 7.

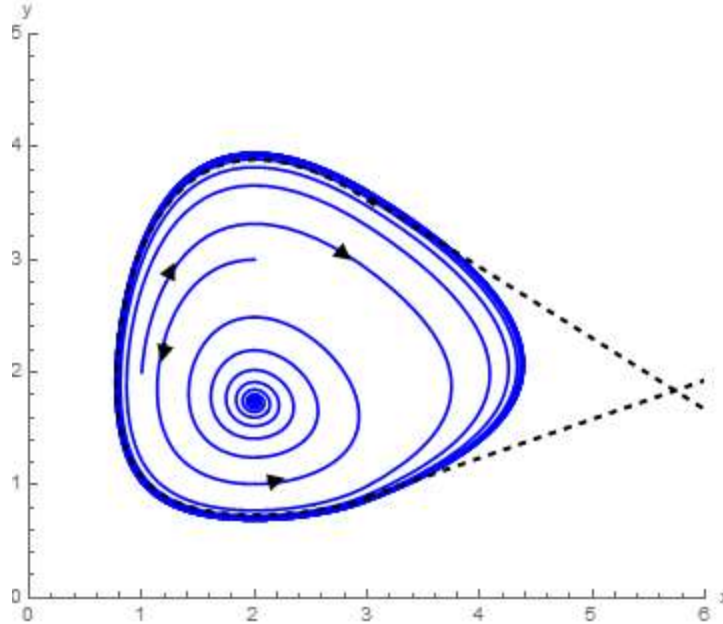


Figure 7: If $\alpha = \frac{1}{15}$ the equilibrium point $S_3 = (2, \frac{26}{15})$ is a stable spiral point in positive time.

For any initial value, whether taken from R_1 or R_2 the solution of System (1) results in a limit cycle in negative time ($-100 \leq t \leq 0$). Figure 8a shows a trajectory tending to a limit cycle when the initial value (2, 3) taken from R_1 is used, while Figure 8b is the result when initial value (4, 4) taken from R_2 is used.

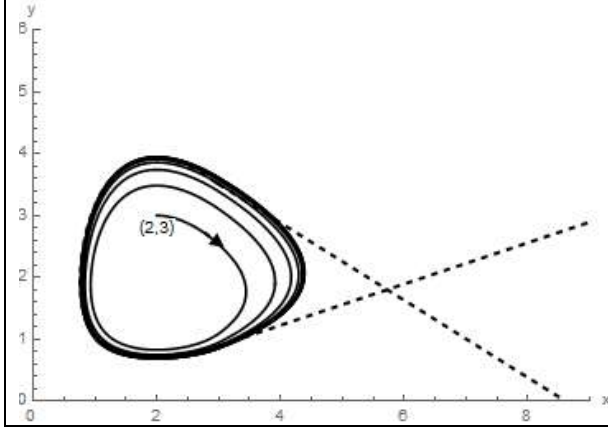


Figure 8a: A trajectory initiated at $(2, 3)$ on the inside of curve C tends to a limit cycle.

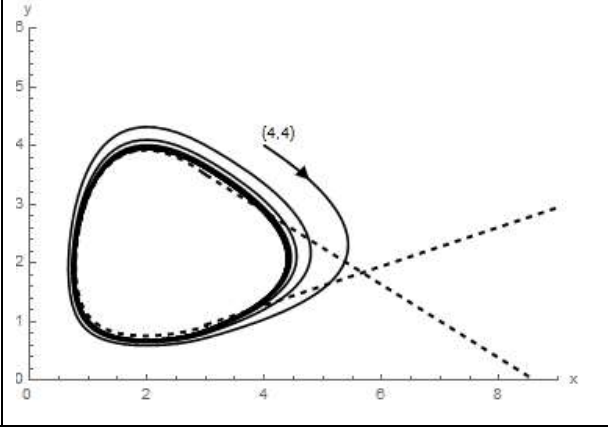


Figure 8b: A trajectory initiated at $(4, 4)$ on the outside of curve C tends to the same limit cycle

For any initial value taken from R_2 or above L_3 , the solutions of System (1) will form a second limit cycle in positive time ($0 \leq t \leq 100$). The second limit cycle is generated with initial value $(5, 4)$ taken from R_2 (Figure 9a) and $(10, 8)$ from the region above L_3 (Figure 9b) respectively.

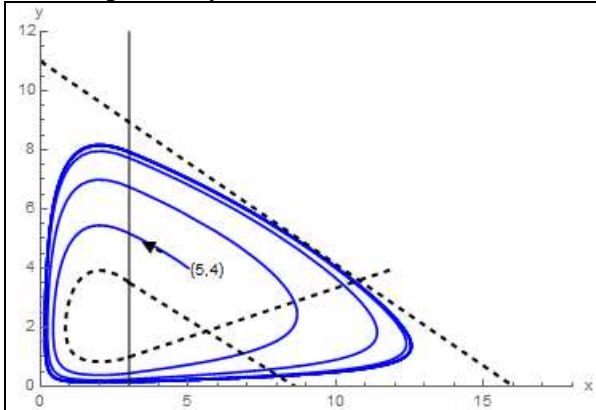


Figure 9a: Limit cycle formed with initial value $(5, 4)$ taken from R_2

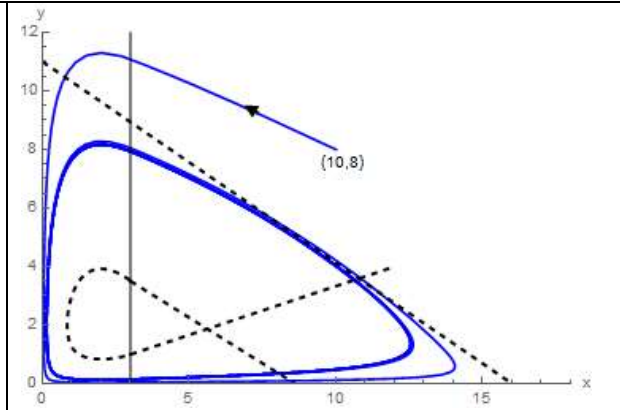


Figure 9b: Limit cycle formed with initial value $(10, 8)$ taken from above L_3 .

In Figure 10 initial values were taken from all three regions, R_1 , R_2 and the region above L_3 , describing the behavior of the trajectories in positive time.

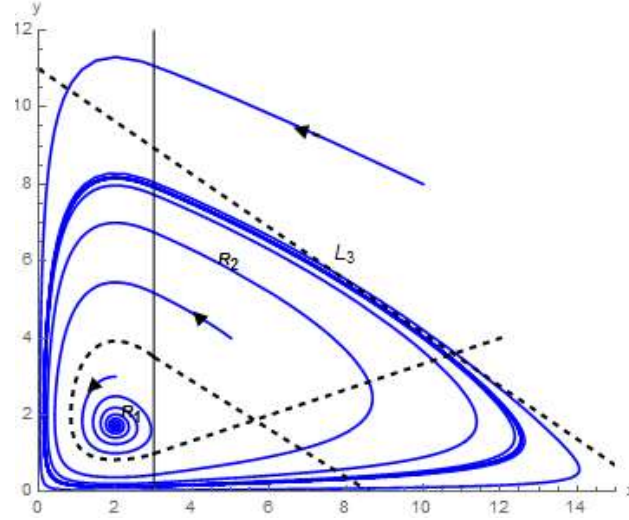


Figure 10: Trajectories of System (1) in positive time.

Finally, in Figures 11a and 11b the formation of the two limit cycles formed by System (1) is shown.

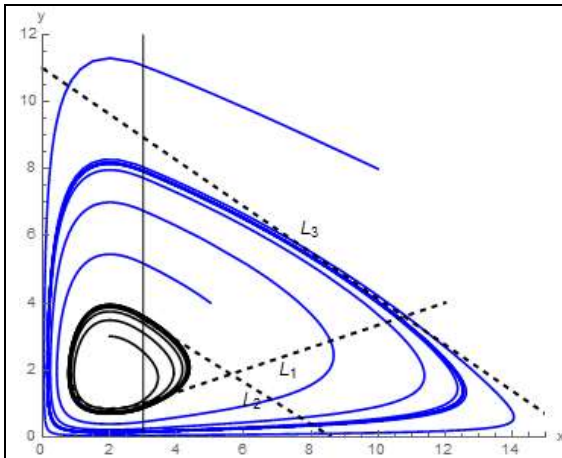


Figure 11a: Two limit cycles formed by generating trajectories in negative and positive time, respectively.

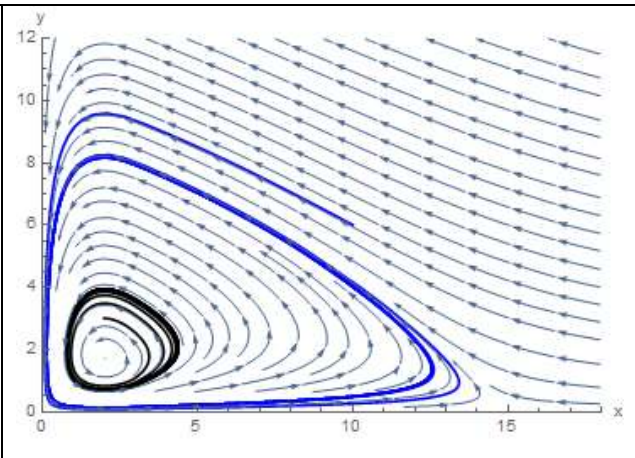


Figure 11b: The vector field of System (1)

Further studies

As long as $0 < \alpha \ll 1$, the closed curve C will exist and therefore no vector field of System (1) will enter the region R_1 . This begs the question: how “small” must α be? In our example the value of $\alpha = 1/15$ was chosen arbitrarily and the existence of two limit cycles was evident.

With some experimentation it seems that for $\alpha = 1/13$ both limit cycles still exist. However, for $\alpha = 1/12$, the results change drastically. Running t from 0 to 500 with initial value (10,6)

the trajectory “passes” through the “limit cycle” spiraling in towards the stable equilibrium as shown in Figure 12.

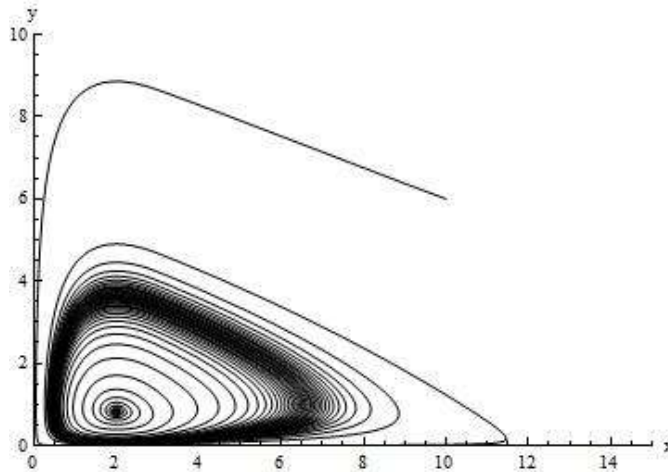


Figure 12: If $\alpha = 1/12$ then the equilibrium becomes a stable spiral.

Further experimentation on the value of α may offer a valuable route of exploration.

Furthermore, Dubois and Closset [1] found evidence on computer that System (1) have two limit cycles and the paper by Yongtai and Li [2] does a qualitative study and proves that this is indeed the case under certain conditions namely $k_3 - \beta k_2 \tau < 0$ and $k_1 + k_3 - \beta k_2 \tau > 0$. We know that no limit cycle is possible should $k_3 - \beta k_2 \tau \geq 0$ but what if $k_3 - \beta k_2 \tau < 0$ and $k_1 + k_3 - \beta k_2 \tau < 0$. Initial experimentation indicates that we still have two limit cycles, but this has not been investigated further in this article.

Conclusion

By unpacking the model an example of basic research is given that should be of value to a young academic interested in biomathematics. The knowledge and expertise gained through critical reading of an article requiring knowledge from more than one discipline should be invaluable. Aspects of modeling and ecology are touched upon as well as technological prowess, differential equations and vector analysis. The exposition presented here should be within the grasp of either someone schooled in biology with basic understanding of differential equations or someone schooled in mathematics and venturing into applications in modeling and biology.

The untangled mathematics mechanism of a model dating from the 1980's combined with rich illustrations, presented here, moves the dated cryptic exposition of a distinct model into the current paradigm of technology use in advancing the field of biomathematics.

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