The Linear Stability Analysis and the Existence of a Limit Cycle of a Predator-Prey System with Holling Type II Functional Response

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Abstract

The main purpose of this paper is to study the long time behavior of a predator-prey model with Holling type II functional response.We prove that the predators can not survive on the prey if the carrying capacity k is relatively small. This gives a critical value of the carrying capacity which can support a predator: k must be larger than the critical value for a coexistence of prey and predator. We prove that the prey and predator can co-survive either on a constant coexistence rate (stable positive equilibrium) or on a periodic oscillation (limit cycle) when k is relatively large. A detailed linear stability analysis is conducted for equilibrium solutions. Finally numerical simulations by MATLAB are used to illustrate the possible solutions which have been analytically proved to exist.

Key word: Predator-prey model; Limit cycle; Coexistence equilibrium; Linear stability analysis.
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1 Introduction

Population dynamics are essential to understand the population interactions in mathematics biology. The Lotka-Volterra systems [3] are first order, nonlinear, differential equations that describe the interaction between two biological species. There are three main types of population interaction: predator-prey, competition, and mutualism [13]. Suppose that two different species of animals interact in the same environment. And suppose further that the first species (prey) only eats vegetation and the second species (predator) eats only the first species. This is an example of predator-prey system [23] and the research described in this paper focuses on predator-prey systems.

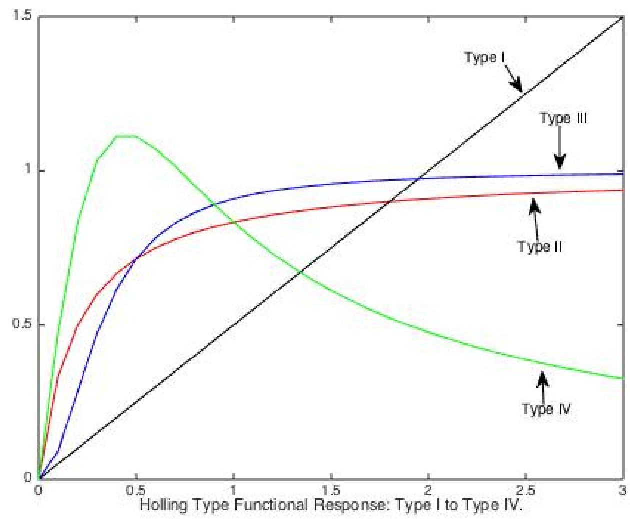

Figure 1: The four types of Holling type functional response.

In the 1950s, Holling conducted experiments to investigate how a predator's rate of prey capture is related to prey density. This relationship called functional response was first introduced by Solomon in the late 1940s [15]. Holling identified classes of functional response: Type I, Type II, and Type III. In 1981, Type IV was introduced by Sokol and Howell (Fig. 1) [7, 17].

Functional response Holling Type I is characterized by a linear increase function which is unbounded. The rate of consumption per predation is proportional to the prey density. This functional response was assumed by Lotka and Volterra in their work on predator-prey interactions [7, 8, 13]. In functional response Type II the number of prey consumed by predation increases rapidly, then plateaus with increasing prey density. Functional response type III is similar to type II except the predator response to the prey decelerates at satiation. In 1977, Real [15] made the connection between predation by animals and catalysis by enzymes. The behavior occurs when a gradient of the curve first increases then decreases with increasing prey density [7, 8, 15]. Holling Type IV functional response was proposed by Sokol and Howell [17]. Later it was called Holling Type IV in [14, 16] and has been studied in [4, 22]. Holling Type IV functional response is different from Type I, Type II and Type III which are monotone functions but Holling Type IV is not. Holling Type IV increases and then decreases to zero as population of prey goes large.

Many different predator-prey models have been studied over the years. Earlier models studied focused on the Lotka-Volterra systems with Holling type I but more realistic models that were studied had a Holling type II or others. Sugie, Kohno, and Miyazaki [19] studied a general predator-prey model with a functional response. They used results from Kuang and Freedman [12] to prove the existence of one limit cycle.

Liu and Chen[21] studied a Holling type II predator-prey model with periodic constant impulsive immigration of the predator. The oscillations were studied numerically and with increasing immigration, the model experiences quasi-oscillating, periodic cascade, chaos, and periodic doubling cascade.

Agiza, ELabbasy, EL-Metwally, and Elsadany [2] studied a discrete predator-prey model by finding equilibrium point, studying the dynamic behavior of the model and constructing numerical simulations. It was found that the linear stability analysis was stable, unstable, saddle, non-hyperbolic. Numerical simulations show that the model displays rich dynamics compare to a continuous model. Their model exhibits chaotic and complex phenomenon.

If spatial spread of species is taken into consideration, a reaction-diffusion partial differential equation can be introduced to describe the distribution of density functions of prey and predator. The spread can lead to many interesting spatial patterns due to the dispersal of species in search for food, and also due to refuge from predators. Among the various pattern formations, Turing patterns are generated when the species in the food chain have different diffusion interactions. There are many research papers which studied spatial pattern formations for predator-prey model with Holling Type II functional response [4, 11, 14, 16, 20, 22]. More references can be found therein.

The main purpose of this research is to study and understand this system by finding the equilibrium points, conducting a linear stability analysis, proving if a limit cycle exist and constructing numerical simulations for the predator-prey model:

$$(1) \qquad \begin{cases} \frac{dU}{dS} = RU(1 - \frac{U}{k} - \frac{EMV}{a+U}) \\ \\ \frac{dV}{dS} = V(\frac{MU}{a+U} - C) \end{cases}$$

where U, V represent the density of the prey and the predator respectively. The assumptions for model (1) are:

- R is the intrinsic growth rate of the prey;
- k is the carrying capacity of the prey;
- E is the relative loss of prey due to the predation;
- C is the the death rate of the predator;
- a is the half-saturation constant of the predator;
- M is the maximum growth rate of the predator and $\frac{U}{a+U}$ represents the Holling Type II functional response.

By letting $b = \frac{M}{R}$, $c = \frac{C}{R}$, $t = RS$, $x = U$, and $y = \frac{EM}{R}V$, model (1) can be rewritten as,

$$(2) \qquad \begin{cases} \frac{dx}{dt} = x(1 - \frac{x}{k} - \frac{y}{a+x}) \\ \\ \frac{dy}{dt} = y(\frac{bx}{a+x} - c) \end{cases}$$

where a, b, c, and k are all positive constants. The main results can be summarized as follows.

Theorem 1.1. *Assume the parameters a, b, c, k are all positive constants in the predator-prey system* (2).

1. *If $k \leq \frac{ac}{b-c}$, there exist two equilibrium solutions. The trivial equilibrium $(0,0)$ is a saddle node and $(k,0)$ is linearly stable.*
2. *If $k > \frac{ac}{b-c}$, there exist three equilibrium solutions. Both the trivial equilibrium $(0,0)$ and $(k,0)$ are saddle nodes. $(x^*, y^*) = \left(\frac{ac}{b-c}, \left(1 - \frac{ac}{k(b-c)}\right)\left(\frac{ab}{b-c}\right)\right)$ is the third positive equilibrium solution.*
    - *If $\frac{ac}{b-c} < k < \frac{a(b+c)}{b-c}$, the positive equilibrium solution (x^*, y^*) is stable.*
    - *If $k = \frac{a(b+c)}{b-c}$, the positive equilibrium solution (x^*, y^*) is a center.*
    - *$k > \frac{a(b+c)}{b-c}$, the positive equilibrium solution (x^*, y^*) is unstable.*
3. *The system has a unique stable limit cycle if and only if $k > \frac{a(b+c)}{b-c}$.*

The paper is organized as follows. In section 2, we present the equilibrium solutions of the model and we conduct the linear stability analysis for the positive coexistence equilibrium. In section 3, we prove the existence of limit cycles under some suitable conditions. In section 4, numerical simulation is to illustrate the rich dynamical phenomena and the existence of limit cycles.

2 Equilibrium and Linear Stability Analysis

Theorem 2.1. *Assume the parameters a, b, c, k are all positive constants in the predator-prey system* (2). *If the following condition is satisfied,*

$$k(b-c) > ac, \tag{3}$$

then there exist three nonnegative equilibrium points for model (2) *and they are* $(0,0)$, $(k,0)$, *and* $\left(\frac{ac}{b-c}, \left(1 - \frac{ac}{k(b-c)}\right)\left(\frac{ab}{b-c}\right)\right)$.

Remark 2.2. It is easy to know that $b > c$ if condition (3) is satisfied, i.e. the relative growth rate of the predator is greater than its relative death rate. $(0,0)$ is a trivial extinction solution of the predator-prey system. $(k,0)$ is a solution where predator is extinct while prey attains its maximum capacity. The unique coexistence state is the third equilibrium solution.

Proof. To find the equilibrium solutions we must solve the algebraic equations for

$$(4) \qquad \begin{cases} x(1 - \frac{x}{k} - \frac{y}{a+x}) = 0 \\ y(\frac{bx}{a+x} - c) = 0 \end{cases}$$

It is easy to find the equilibrium solutions $(0,0)$ and $(k,0)$. The coexistence equilibrium solution is obtained by solving

$$(5) \qquad \begin{cases} (1 - \frac{x}{k} - \frac{y}{a+x}) = 0 \\ (\frac{bx}{a+x} - c) = 0. \end{cases}$$

From second equation in (5) we have

$$x = \frac{ca}{b-c}.$$

Substituting $x = \frac{ca}{b-c}$ into the first equation in (5), it gives rise to the coexistence equilibrium solution $\left(\frac{ac}{b-c}, \left(1 - \frac{ac}{k(b-c)}\right)\left(\frac{ab}{b-c}\right)\right)$. ☐

Theorem 2.3. *Assume the parameters a, b, c, k are all positive constants in the predator-prey system (2). Let*

$$(6) \qquad \alpha = (b-c) - \frac{ac}{k},$$

$$(7) \qquad \beta = \frac{c}{b(b-c)^2}\left(\alpha - \frac{ab}{k}\right)^2 - 4\alpha,$$

and

$$(8) \qquad \delta = \alpha - \frac{ab}{k}.$$

Assume $b > c$ and $\alpha > 0$. There are exactly five cases for the linear stability of the positive equilibrium point $(x^*, y^*) = \left(\frac{ac}{b-c}, \left(1 - \frac{ac}{k(b-c)}\right)\left(\frac{ab}{b-c}\right)\right)$ for the system (2).

1. *If $\beta < 0$ and $\delta = 0$, the positive equilibrium point (x^*, y^*) is a center.*
2. *If $\beta < 0$ and $\delta > 0$, the positive equilibrium point (x^*, y^*) is an unstable spiral.*
3. *If $\beta < 0$ and $\delta < 0$, the positive equilibrium point (x^*, y^*) is a stable spiral.*
4. *If $\beta \geq 0$ and $\delta > 0$, the positive equilibrium point (x^*, y^*) is linearly unstable.*
5. *If $\beta \geq 0$ and $\delta < 0$, the positive equilibrium point (x^*, y^*) is linearly stable.*

Proof. Since (x^*, y^*) is an equilibrium solution of the ODE system (2), $f(x^*, y^*) = 0$ and $g(x^*, y^*) = 0$, where

$$\begin{cases} f(x,y) = x(1 - \frac{x}{k} - \frac{y}{a+x}), \\ g(x,y) = y(\frac{bx}{a+x} - c). \end{cases} \tag{9}$$

By the theory of linear stability for ODE system, the linear stability of equilibrium is determined by the linearized system

$$\frac{d\xi}{dt} = J\xi, \tag{10}$$

where J is the Jacobian matrix at the equilibrium (x^*, y^*),

$$J = \left. \begin{pmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \end{pmatrix} \right|_{(x^*, y^*)} \tag{11}$$

By direct computation the Jacobian matrix for system at the equilibrium (x^*, y^*) is

$$J = \left. \begin{pmatrix} 1 - \frac{2x}{k} - \frac{ay}{(a+x)^2} & \frac{-x}{a+x} \\ \frac{aby}{(a+x)^2} & \frac{bx}{a+x} - c \end{pmatrix} \right|_{(x^*, y^*)} \tag{12}$$

$$= \begin{pmatrix} \frac{c}{b} - \frac{ac(b+c)}{bk(b-c)} & -\frac{c}{b} \\ (b-c) - \frac{ac}{k} & 0 \end{pmatrix}. \tag{13}$$

The characteristic equation of the Jacobian matrix is computed by $\det(\lambda I - J) = 0$ where I is the identity matrix. It is

$$\left(\lambda - \left(\frac{c}{b} - \frac{ac(b+c)}{bk(b-c)}\right)\right)\lambda - \left((b-c) - \frac{ac}{k}\right)\left(\frac{-c}{b}\right) = 0$$

$$\lambda^2 - \left(\frac{c}{b} - \frac{ac(b+c)}{bk(b-c)}\right)\lambda + \left((b-c) - \frac{ac}{k}\right)\left(\frac{c}{b}\right) = 0$$

To solve for the general solutions we let

$$A_1 = -\left(\frac{c}{b} - \frac{ac(b+c)}{bk(b-c)}\right),$$

and

$$A_2 = \left((b-c) - \frac{ac}{k}\right)\left(\frac{c}{b}\right).$$

We have the quadratic equation

$$\lambda^2 + A_1\lambda + A_2 = 0.$$

By applying quadratic formula, we obtain

$$\lambda_{1,2} = \frac{-A_1 \pm \sqrt{A_1^2 - 4A_2}}{2}.$$

Generally, there are six cases for the stability analysis of an equilibrium solution:
If $A_1^2 - 4A_2 < 0$ then the eigenvalues λ_1 and λ_2 are complex.

1. If $A_1 = 0$, then the eigenvalues λ_1 and λ_2 are two conjugate complex with zero real parts. Therefore the positive equilibrium (x^*, y^*) is a center node.

2. If $A_1 < 0$, then the eigenvalues λ_1 and λ_2 are two conjugate complex with positive real parts. Therefore the positive equilibrium (x^*, y^*) is a unstable spiral.

3. If $A_1 > 0$, then the eigenvalues λ_1 and λ_2 are two conjugate complex with negative real parts. Therefore the positive equilibrium (x^*, y^*) is a stable spiral.

If $A_1^2 - 4A_2 \geq 0$ then the eigenvalues λ_1 and λ_2 are real.

4. If $A_1 < 0$, then the eigenvalues λ_1 and λ_2 are two positive real numbers. Therefore the positive equilibrium (x^*, y^*) is linearly unstable.

5. If $A_1 > 0$ and $A_2 > 0$, then the eigenvalues λ_1 and λ_2 are two negative real numbers. Therefore the positive equilibrium (x^*, y^*) is linearly stable.

6. If $A_1 > 0$ and $A_2 < 0$, then the eigenvalues λ_1 and λ_2 have two real numbers with different signs. Therefore the positive equilibrium (x^*, y^*) is saddle.

By using the definition α in (6), β in (7) and δ in (8), we rewrite

$$A_1 = \frac{-\delta c}{b(b-c)},$$

$$A_2 = \frac{c}{b}\alpha$$

and

$$A_1^2 - 4A_2 = \frac{c}{b}\beta.$$

By the assumption $b > c$ and $\alpha > 0$, we have $A_2 > 0$. So the case 6 above does not hold. By direct computation, the first five cases above are equivalent to the results in the theorem. The proof is competed.

□

By similar arguments, it is easy to prove the following linear stability results for equilibrium solutions $(0, 0)$ and $(k, 0)$ and the proof is omitted.

Theorem 2.4. *Assume the parameters a, b, c, k are all positive constants in the predator-prey system* (2)*. The equilibrium solution* $(0, 0)$ *is a saddle node.*

Theorem 2.5. *Assume the parameters a, b, c, k are all positive constants in the predator-prey system* (2)*. The linear stability for the equilibrium point* $(x^*, y^*) = (k, 0)$ *will have two cases.*

1. *The equilibrium be will be stable when k is less than or equal to $\frac{ac}{b-c}$.*
2. *The equilibrium be will be saddle if k is greater than $\frac{ac}{b-c}$.*

3 Existence of Limit Cycles

Many attempts have been made to prove the existence and uniqueness of limit cycles for the predator-prey system (1). Hsu, Hubbell and Waltman [9, 10] studied a system of two predator species competing exploitatively for the same prey population. It was focused on the question as to when the competitive exclusion principal holds, given the growth parameters of the prey and the functional response parameters of the two predators. They found out that the solution behavior of the competing predator system mainly depends on a single predator-prey system which is essentially equivalent to the system (1) of the predator-prey with Holling type II functional response up to irrelevant constants. In [9], they proved that there exists at least one limit cycle in the first quadrant of the phase pane. If the limit cycle is unique, it is stable. In [10], they conjectured that the limit cycle is unique. In [5], the uniqueness of the limit cycle for the system (1) was proved and the result of uniqueness of a limit cycle was extended in a more general predator-prey model in [6, 12, 19]. The following theorem is an immediate consequence of the papers [5, 6, 9, 10, 12, 19] but the results in those papers are stated in a slightly different form.

Theorem 3.1. *Assume the parameters a, b, c, k are all positive constants in the predator-prey system* (2)*. The system has a unique stable limit cycle if and only if :*

$$a(b + c) < k(b - c). \tag{14}$$

Remark 3.2. The conditions in theorem 3.1 can imply that all three equilibriums are unstable. By theorem 2.4, $(0, 0)$ is a saddle node. Since $a(b+c) < k(b-c)$ implies $ac < k(b-c)$, $(k, 0)$ is a saddle node by theorem 2.5. If $a(b+c) < k(b-c)$, we have $b > c$, $\alpha > 0$ and $\delta > 0$. By theorem 2.3, the coexistence positive equilibrium is also unstable. The main results in theorem 1.1 is an immediate consequence of the above theorems.

4 Numerical Simulation

In this section numerical simulation of the model (2) is done using MATLAB (R2013a) computer program. Instead of choosing the prey capacity k as a parameter as in theorem

1.1, we pick a as a parameter in example 1 and example 2 to illustrate the linear stability of the positive equilibrium solution under the influence of the half saturation of predator. The positive constants b, c, and k are fixed at certain values and the value of a is computed to classify the positive equilibriums. The different types of linear stability are observed.

4.1 Example 1

Let $b = 51$, $k = 40$, and $c = 1$. The positive equilibrium solution in theorem 2.1 with parameter a is

$$(x^*, y^*) = \left(\frac{a}{50}, \left(1 - \frac{a}{200}\right)\frac{a}{50}\right).$$

For the equilibrium to be positive we have $0 < a < 200$. The values of α, β, and δ in theorem 2.3 are easy to find.

$$\alpha = 50 - \frac{a}{40}.$$

$$\beta = \frac{1}{51(50)^2}\left(50 - \frac{52a}{40}\right)^2 - 4\left(50 - \frac{a}{40}\right).$$

$$\delta = 50 - \frac{52a}{40}.$$

When $0 < a < 200$, it is easy to show $\beta < 0$. By theorem 2.3 we have three cases:

1. When $a = \frac{2000}{52}$, we have $\beta < 0$, $\delta = 0$, and the positive equilibrium is a center (see Figure 2).

2. When $\frac{2000}{52} < a < 200$, we have $\beta < 0$, $\delta < 0$, and the positive equilibrium is a stable spiral (see Figure 3).

3. When $0 < a < \frac{2000}{52}$, we have $\beta < 0$, and $\delta > 0$, and the positive equilibrium is a unstable spiral (see Figure 4).

In Figure 2, $a = \frac{2000}{52}$ and the positive equilibrium $(.7692, 38.4763)$ is a center. In figure B, the initials of the solutions are $(0.3, 38)$, $(0.4, 38)$, $(0.5, 28)$, $(0.7, 38)$, and $(0.8, 38)$ respectively. In figure A, the solution curve is a periodic trend for both the predator and prey.

In Figure 3, $a = \frac{2000}{52} + 25$ and the positive equilibrium $(1.2692, 62.6768)$ is a stable spiral. The trajectory starting with the initial value $(1.7, 86)$ converges to the equilibrium solution spirally.

In Figure 4, $a = \frac{2000}{52} - 15$ and the positive equilibrium $(0.5, 24)$ is unstable spiral. We picked an initial value close to equilibrium point. Its trajectory in the phase plane diverges away from the equilibrium.

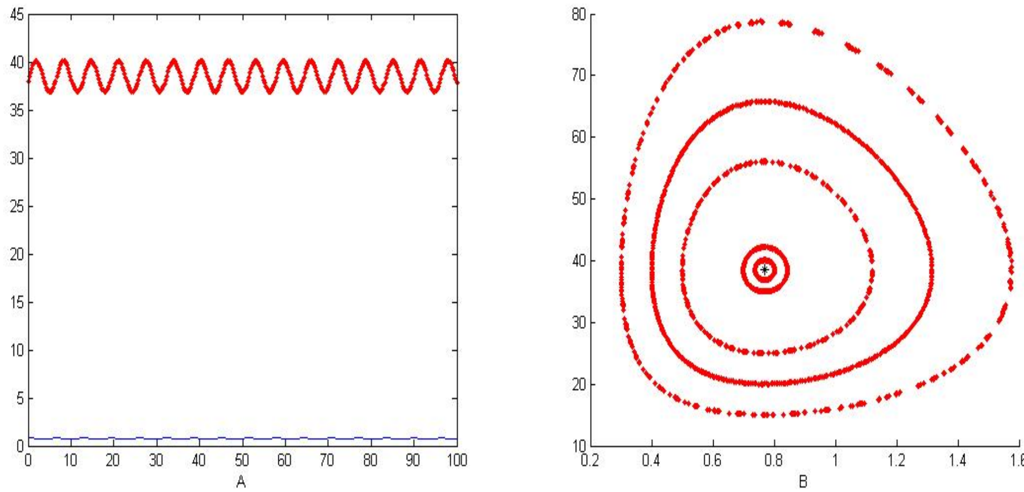

Figure 2: Figure A is the solution curve with respect to time where the solid line represents the prey and dash line represents the predator for the initial value $(0.8, 38)$. Figure B is the center phase portrait near the positive equilibrium $(x^*, y^*) = (0.7692, 38.4763)$.

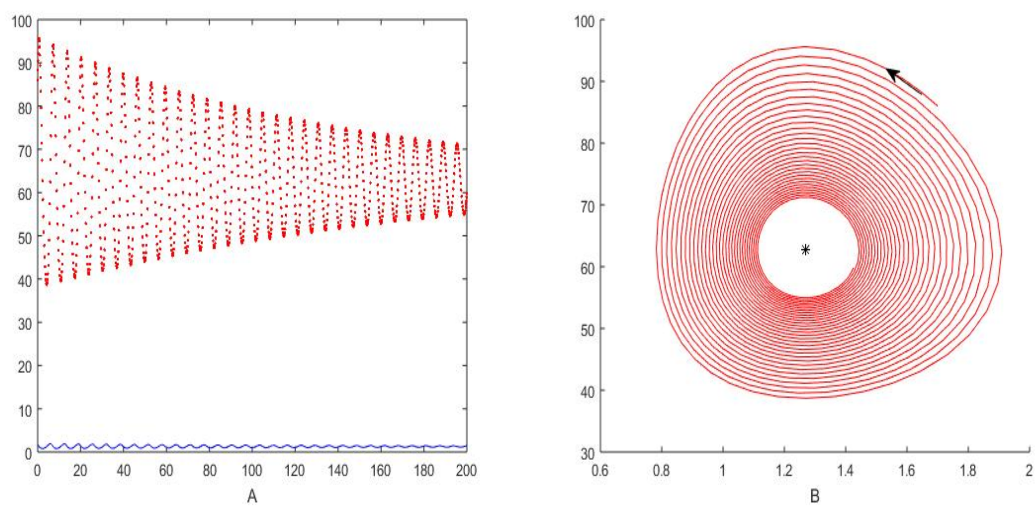

Figure 3: Figure A is the solution curve with respect to time where the solid line represents the prey and dase line represents the predator for the initial value $(1.7, 86)$. Figure B is the stable spiral phase portrait for $(x^*, y^*) = (1.2692, 62.6768)$.

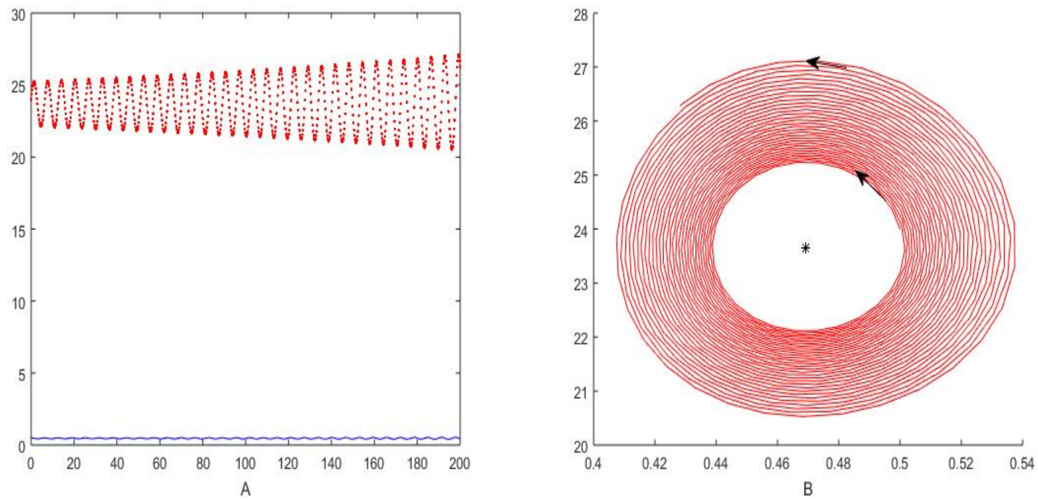

Figure 4: Figure A is the solution curve with respect to time where the solid line represents the prey and dase line represents the predator for the initial value $(0.5, 24)$. Figure B is the unstable spiral phase portrait for $(x^*, y^*) = (0.4692, 23.6500)$.

4.2 Example 2

Similar to example 1, we fixed the parameters for $b = 5$, $k = 50$, and $c = 4.99$, where growth rate b and death rate c of predator are very close to each other. The positive equilibrium solution with parameter a is

$$(x^*, y^*) = \left(499a, \left(1 - \frac{499a}{50}\right) 500a\right).$$

For the equilibrium to be positive we have $0 < a < \frac{50}{499} \approx 0.1002$. The values of α, β, and δ in theorem 2.3 are

$$\alpha = 0.01 - \frac{4.99a}{50},$$

$$\beta = \frac{4.99}{5(0.01)^2}\left(.01 - \frac{9.99a}{50}\right)^2 - 4\left(.01 - \frac{4.99a}{50}\right),$$

and

$$\delta = .01 - \frac{9.99a}{50}.$$

If $a = \frac{50}{999} \approx 0.0501$, $\delta = 0$. By using quadratical formula, we have $\beta < 0$ when $.0424 < a < 0.0567$ (see figure 5).

By theorem 2.3 we have five cases:

1. When $0.0567 < a < 0.1002$, the positive equilibrium is linearly stable (see Figure 6).

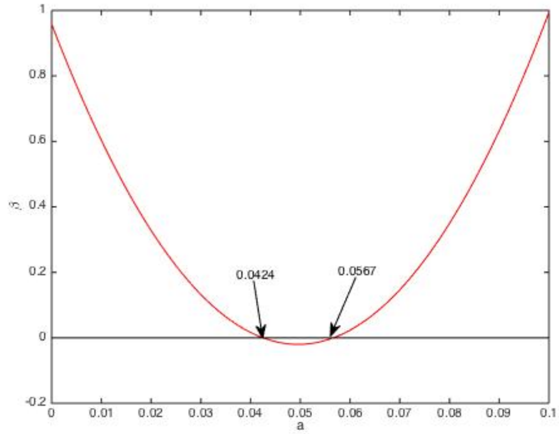

Figure 5: This graph shows how we determined the parameters of a in example 2 by finding the the x-intercepts of β.

2. When $0 < a < 0.0424$, the positive equilibrium is linearly unstable (see Figure 7).

3. When $0.0424 < a < 0.0501$, the positive equilibrium is unstable spiral.

4. When $a = .05001$, the positive equilibrium is a center.

5. When $.0501 < a < .0567$, the positive equilibrium is stable spiral.

In Figure 6, $a = 0.0580$ and the equilibrium solution $(x^*, y^*) = (28.9420, 12.2136)$ is linearly stable. Figure A shows the prey population will increase then over time converges to a population density. Similarly, the predator population density will converge. Both prey and predator will live in coexistence.

In Figure 7, $a = 0.0325$ and the equilibrium point $(x^*, y^*) = (16.2175, 10.9793)$ is linearly unstable. The trajectory diverges away from the positive equilibrium solution. Moreover, it converges to the stable equilibrium solution $(k, 0) = (50, 0)$.

We do not give numerical simulations for other three cases because they are similar to the cases in example 1.

4.3 Limit Cycle

Let $a = 10$, $b = 5$, $k = 50$, and $c = 2$. Then the condition in theorem (3.1) is fulfilled and there exist a stable limit cycle. In Figure 8, the initial value $(35, 11)$ is chosen to be close to the equilibrium point $(x^*, y^*) = (34.9300, 10.5490)$. The trajectory from the initial value approaches the limit cycle.

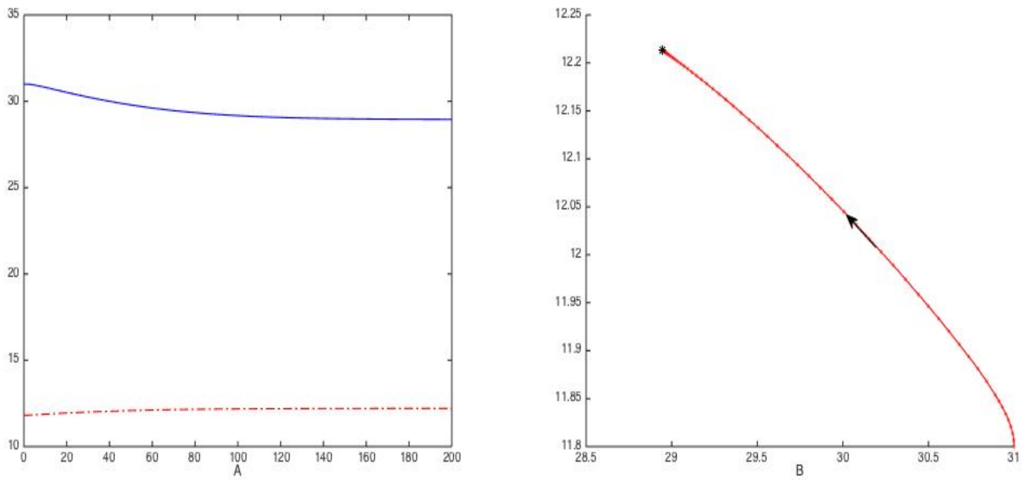

Figure 6: Figure A is the solution curve with respect to time where the solid line represents the prey and dash line represents the predator for the initial value $(31, 11.8)$. Figure B shows that the trajectory converges to the positive equilibrium solution $(x^*, y^*) = (28.9420, 12.2136)$

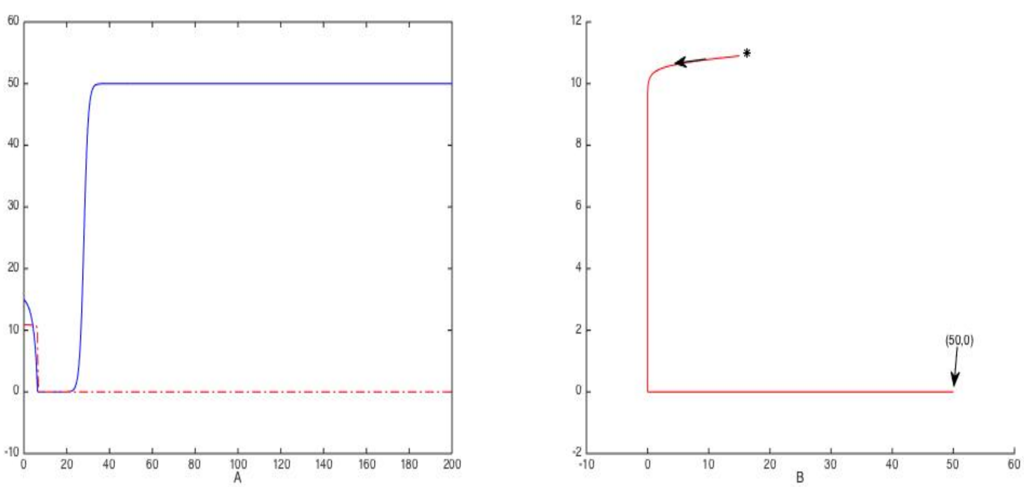

Figure 7: Figure A is the solution curve with respect to time where the solid line represents the prey and dash line represents the predator for the initial value $(15, 10.9)$. Figure B shows that the trajectory diverges away form the positive equilibrium $(x^*, y^*) = (16.2175, 10.9793)$ but it converges to another equilibrium $(k, 0) = (50, 0)$.

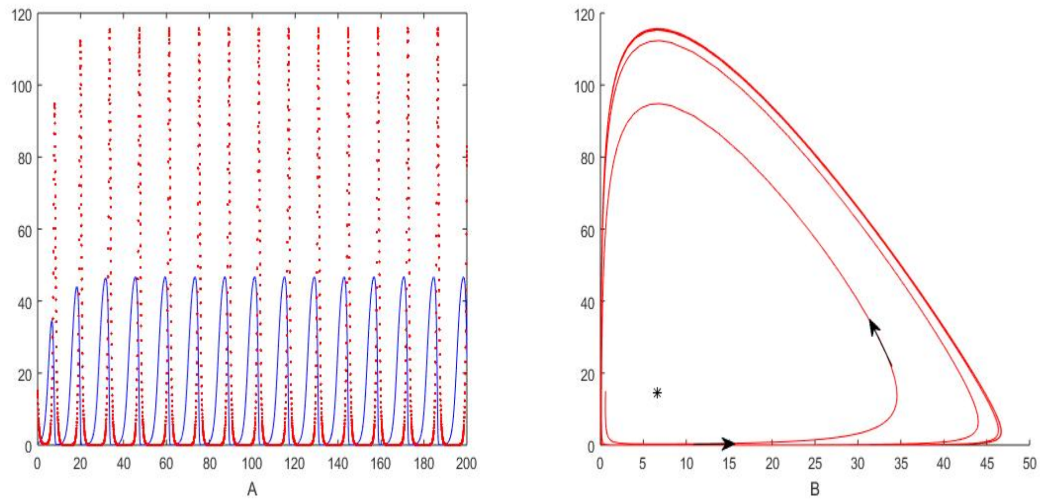

Figure 8: Figure A is the solution curve with respect to time where the solid line represents the prey and dase line represents the predator for the initial value $(35, 11)$. Figure B is the limit cycle for the equlibrium point $(x^*, y^*) = (34.9300, 10.5490)$

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