

Uniqueness of Limit Cycles in a Predator-Prey Model with Sigmoid Functional Response*

André Zegeling^{1,†}, Hailing Wang¹ and Guangzheng Zhu²

Abstract In this paper, we prove that a predator-prey model with sigmoid functional response and logistic growth for the prey has a unique stable limit cycle, if the equilibrium point is locally unstable. This extends the results of the literature where it was proved that the equilibrium point is globally asymptotically stable, if it is locally stable. For the proof, we use a combination of three versions of Zhang Zhifen’s uniqueness theorem for limit cycles in Liénard systems to cover all possible limit cycle configurations. This technique can be applied to a wide range of differential equations where at most one limit cycle occurs.

Keywords Limit cycle, predator-prey system, Liénard equation, Sigmoid functional response

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1. Introduction

In [15] a predator-prey system was discussed with a sigmoid functional response $p(x)$

$$\begin{aligned}\frac{dx(t)}{dt} &= h(x) - p(x)y, \\ \frac{dy(t)}{dt} &= -\mu y + \beta p(x)y\end{aligned}\tag{1.1}$$

with $h(x) = rx(1 - \frac{x}{K})$ and $p(x) = \frac{x^2}{a+bx+cx^2}$.

The parameters are real and positive. The growth of the prey population is chosen to be logistic with r , the intrinsic growth rate and K , the carrying capacity. The parameter μ is the predator death rate, and β is the constant conversion rate of the predator after eating the prey. The parameters a , b and c in the functional response do not have an obvious biological meaning and are considered to be fit

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through a phenomenological approach based on observed data, a method followed by Holling in [8].

This type of functional response for a predator-prey model was first introduced by Holling in his ground-breaking paper [8]. The typical approach in predator-prey systems is to take a functional response which is monotonically increasing as a function of the prey density, bounded and without inflection points, e.g., the Holling II functional response function.

However, recently, more research has been done on the case where the functional response has a sigmoid shape with one inflection point. The functional response in this paper can be seen as a generalization of the Holling III functional response. Other variations of this response function similar to the one in this paper can be found in [1–7, 9, 10, 13].

It is assumed that system (1.1) has a positive equilibrium point A with $x^* > 0$ and $y^* > 0$ such that $h(x^*) - p(x^*)y^* = 0$, $-\mu + \beta p(x^*) = 0$ (here, positive refers to the fact that the prey and predator density have a positive value). It is not difficult to see that A is unique when it exists. In the following, we will always assume that the parameters of the system are such that there is exactly one positive equilibrium point A , because the dynamics of the system become trivial without it.

The main result of [15] was the proof that the system is globally asymptotically stable, when A is locally stable. Effectively, this follows from the fact that the system does not have limit cycles, is bounded and does not have attracting equilibrium points on the coordinate axes in the phase plane.

The aim of this paper is to show that system (1.1) has exactly one limit cycle, if A is locally unstable. In the process, we will give a simplified proof of the result in [15] for the non-existence of the limit cycle, when A is locally stable. The methods we use are a combination of three flavours of Zhang Zhifen's theorem. The reason three different versions are needed is that the divergence of the associated Liénard system is zero on two vertical lines in the phase plane. Since it is not known a priori which of these lines will be crossed by a limit cycle, different configurations need to be considered. In each case, a different version of Zhang Zhifen's theorem is needed.

From a mathematical point of view, the choice of a sigmoidal functional response function is related to a question discussed in a few papers [11, 12, 16], where the influence of the convexity of the functional response function on the number of limit cycles was explored. For example, it was shown in [16] that a functional response function with a change in convexity, similar to a sigmoidal function, leads to more limit cycles than the case where it is just concave down. On the other hand, in [12], the cases were observed with more than one limit cycle in the concave down case. This paper shows that even in a class with a sigmoidal functional response function that is more general than the traditional Holling III function, not more than one limit cycle will occur. This suggests that it is not necessarily the convexity of the function that is driving the number of limit cycles in a Gause predator-prey system.

In Section 2, we introduce the theorems for limit cycles in Liénard systems which we will use. Section 3 contains the relation between system (1.1) and Liénard systems. In Section 4, we show the non-existence of limit cycles in the case of the stable equilibrium point A . Then, the main result will be given in Section 5, where we show the uniqueness of limit cycles when A is unstable.

2. Liénard systems

One of the most successful approaches in studying the uniqueness of limit cycles in two-dimensional autonomous ordinary differential equations has been the application of Zhang Zhifen's theorem (see [17]). There are different versions of this theorem, and in this section, the versions needed for our proof are summarized.

Definition 2.1. A generalized Liénard system takes the form

$$\begin{aligned}\frac{dx(t)}{dt} &= F(x) - \psi(y), \\ \frac{dy(t)}{dt} &= g(x),\end{aligned}\tag{2.1}$$

defined in a region $x \in (x_-, x_+)$, $y \in (y_-, y_+)$. The divergence of the system $F'(x)$ is traditionally denoted by $f(x)$.

In this section, we summarize the theorems needed to prove the non-existence or uniqueness of limit cycles for system (1.1), after it has been transformed to the Liénard form of (2.1). The first Lemma 2.1 concerns the application of a Dulac-function to prove non-existence in certain cases. The next three theorems 2.1, 2.2, 2.3 are uniqueness theorems which apply to different configurations of the limit cycle. The first theorem 2.1 is a classical result originally due to Zhang Zhifen concerning a limit cycle crossing two vertical lines corresponding to the two zeroes of $f(x)$. The second theorem 2.2 is a stronger theorem which applies to the case, when the limit cycle crosses exactly one vertical line corresponding to a zero of $f(x)$. The third theorem 2.3 is a special case of Theorem 2.2 which can be applied to our system in some situations simplifying the proof.

For the cases where no limit cycles appear, we use the following simple lemma.

Lemma 2.1. *If the functions in (2.1) satisfy the following conditions:*

- (i) $(x - x_g)g(x) > 0$, for $x \neq x_g$;
- (ii) $\exists \lambda \in \mathbb{R}$ such that $f(x) - \lambda g(x)$ has a fixed sign for $x_- < x < x_+$,

then system (2.1) has no limit cycles surrounding the singularity at $x = x_g$ in the strip $x_- < x < x_+$.

This lemma follows from the application of a Dulac-function in the form $B(x, y) = e^{-\lambda y}$ to (2.1). Essentially, the lemma says that if $y = \frac{f(x)}{g(x)}$ has a “gap” (a horizontal line $y = \lambda$ which does not have intersections with the graph of the function), then there are no limit cycles.

Note that for the special case $\lambda = 0$, the lemma states that in order to have limit cycles, the function $f(x)$ needs to have at least one zero and $f(x)$ needs to change sign.

A generalization of Zhang Zhifen's theorem (by Cherkas and Zhilevich) which we will use for proving uniqueness of limit cycles in one case is Theorem 4.9 in [17].

Theorem 2.1 ([17]). *If the functions in (2.1) satisfy the following conditions in the strip $x \in (x_-, x_+)$:*

- (i) $(x - x_g)g(x) > 0$, for $x \neq x_g$;
- (ii) $(x - x_f^{(1)})(x - x_f^{(2)})f(x) < 0$, for $x \neq x_f^{(1)}$, $x \neq x_f^{(2)}$, $x_f^{(1)} < x_g < x_f^{(2)}$;
- (iii) $\frac{d\psi(y)}{dy} > 0$;
- (iv) $\frac{f(x)}{g(x)}$ is non-increasing for $x_- < x < x_f^{(1)}$ and $x_f^{(2)} < x < x_+$,

then the system has at most one limit cycle for $x \in (x_-, x_+)$ enclosing the interval $x_f^{(1)} < x < x_f^{(2)}$, which is stable and hyperbolic, if it exists.

Note that this theorem makes a statement about the uniqueness of limit cycles crossing both vertical lines $x = x_f^{(1)}$ and $x = x_f^{(2)}$, where the function $f(x)$ is equal to zero.

To cover the case where a limit cycle crosses only one vertical line $x = x_f$, where $f(x_f) = 0$, we will use the theorem from [18] (Theorem 3, Page 485).

Theorem 2.2 ([18]). *If the functions in (2.1) satisfy the following conditions in the strip $x \in (x_-, x_+)$:*

- (i) $(x - x_g)g(x) > 0$, for $x \neq x_g$;
- (ii) $(x - x_f)f(x) > 0$, for $x \neq x_f, x_f < x_g$;
- (iii) $\frac{d\psi(y)}{dy} > 0$;
- (iv) *The system of equations*

$$\begin{aligned} F(x_1) &= F(x_2), \\ \frac{f(x_1)}{g(x_1)} &= \frac{f(x_2)}{g(x_2)}, \end{aligned}$$

has at most one solution $x_- < x_1 < x_f, x_g < x_2 < x_+$;

- (v) $\frac{f(x)}{g(x)}$ is decreasing for $x_- < x < x_f$,

then the system has at most one limit cycle for $x \in (x_-, x_+)$, which is stable and hyperbolic, if it exists.

The statement of the theorem remains true, if the zero of $f(x)$ lies to the right of the zero of $g(x)$, i.e., $(x - x_f)f(x) < 0$, for $x \neq x_f, x_f > x_g$. In that case, the function $\frac{f(x)}{g(x)}$ should be decreasing on the interval $x_f < x < x_+$. In other words, the uniqueness of limit cycle will follow, if the function $\frac{f(x)}{g(x)}$ is decreasing on the interval outside the zero of $f(x)$ not containing x_g , and if the system of the equations in (iv) of the theorem has a unique solution.

A special case of this theorem arises when the function $\frac{f(x)}{g(x)}$ is monotonic.

Theorem 2.3. *If the functions in (2.1) satisfy the following conditions in the strip $x_- < x < x_+$,*

- (i) $(x - x_g)g(x) > 0$, for $x \neq x_g$;
- (ii) $(x - x_f)f(x) < 0$, $x \neq x_f, x_f > x_g$;
- (iii) $\frac{d\psi(y)}{dy} > 0$;
- (iv) $\frac{f(x)}{g(x)}$ is nonincreasing in $x_- < x < x_g$ and $x_f < x < x_+$,

then the system has at most one limit cycle for $x \in (x_-, x_+)$, which is stable and hyperbolic, if it exists.

This follows from the fact that if $\frac{f(x)}{g(x)}$ is decreasing, then the system in (iv) in Theorem 2.2 has a unique non-trivial solution.

3. The predator-prey system as a Liénard system

In order to apply the theorems for Liénard systems from the previous section, we need to write (1.1) in the form of a generalized Liénard system.

This is accomplished by performing a simple change of variables $t \rightarrow \frac{t}{p(x)}$, $y = e^v$. System (1.1) takes the form

$$\begin{aligned}\frac{dx(t)}{dt} &= \frac{h(x)}{p(x)} - e^v = \frac{r(1 - \frac{x}{K})(a + bx + cx^2)}{x} - e^v, \\ \frac{dy(t)}{dt} &= -\frac{\mu(a + bx + cx^2)}{x^2} + \beta,\end{aligned}\quad (3.1)$$

i.e., we get a generalized Liénard system (2.1) with (here we restored the variable $v \rightarrow y$):

$$\begin{aligned}\psi(y) &= e^y, \\ F(x) &= \frac{r(1 - \frac{x}{K})(a + bx + cx^2)}{x}, \\ g(x) &= \frac{-\mu a - \mu bx + (\beta - \mu c)x^2}{x^2}, \\ f(x) = F'(x) &= r\left(-\frac{b}{K} + c - \frac{2cx}{K} - \frac{a}{x^2}\right).\end{aligned}\quad (3.2)$$

In system (1.1), limit cycles are restricted to the strip $0 < x < K$, because $\frac{dx}{dt} = -p(K)y < 0$ for $x = K$, and limit cycles cannot cross it.

Therefore, in the application of the theorems of the previous sections, we can take $x_- < x < x_+$ as $0 < x < K$. However, it turns out that $x = K$ does not play a significant role in the proofs, so for notational convenience, we will take $x_+ = \infty$.

Using (3.2) we define the function Z_λ :

$$Z_\lambda(x) = f(x) - \lambda g(x) = \frac{1}{x^2} \left[r \left(\left(-\frac{b}{K} + c \right) x^2 - \frac{2cx^3}{K} - a \right) - \lambda (-\mu a - \mu bx - \sigma x^2) \right] \equiv \frac{1}{x^2} U_\lambda(x), \quad (3.3)$$

where $\sigma = \mu c - \beta$. The important factor in $Z_\lambda(x)$ is $U_\lambda(x)$. Each choice of λ corresponds to scanning the graph of $y = \frac{f(x)}{g(x)}$ with horizontal lines $y = \lambda$: the number of zeroes of $U_\lambda(x)$ indicates the number of intersections.

If there exists a λ such that $U_\lambda(x)$ does not have a zero on the relevant interval for x , then no limit cycles will exist according to Lemma (2.1).

If for all λ , $U_\lambda(x)$ only has simple zeroes, then the function $\frac{f(x)}{g(x)}$ is monotonic which is one of the critical conditions of Theorems (2.1), (2.2), (2.3). This latter property was used in [11] to prove the uniqueness of limit cycles in a different predator-prey system. Moreover, the location of the zeroes of $U_\lambda(x)$ will give information about the possible solutions to the system of equations (iv) in Theorem (2.2).

The function $U_\lambda(x)$ is cubic in x , which restricts the number of zeroes to be 3. If there are three zeroes, then they are necessarily simple. This makes it possible to draw conclusions about the function $\frac{f(x)}{g(x)}$ quickly without doing long calculations.

First, we restrict the parameters of the system to the cases where limit cycles could occur.

Lemma 3.1. *Necessary conditions for the existence of limit cycles in system (3.1) are*

- (i) $f(x)$ has two simple zeroes $x_f^{(1)}$ and $x_f^{(2)}$ with $0 < x_f^{(1)} < x_f^{(2)}$;
- (ii) $g(x)$ has a unique simple zero x_g , with $x_g > 0$.

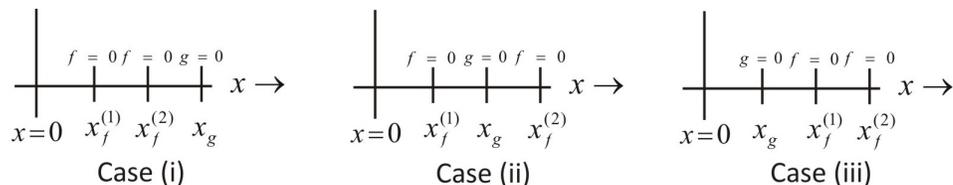


Figure 1. The three cases of Definition 3.1 for the relative position of the zeroes of $f(x)$ and $g(x)$.

These conditions imply that the parameters in (3.3) should satisfy

$$b < cK \quad \text{and} \quad \sigma < 0.$$

Proof. The zeroes of $f(x)$ are determined by the cubic function $H(x) = (-\frac{b}{K} + c)x^2 - \frac{2cx^3}{K} - a$. Therefore, $H(0) = -a < 0$, $H'(0) = 0$, $H''(0) = 2(-\frac{b}{K} + c)$. Since $\lim_{x \rightarrow -\infty} H(x) = \infty$, $\lim_{x \rightarrow \infty} H(x) = -\infty$, if the function has zeroes, then there have to be two for $x > 0$ to ensure the possibility of a change of sign in the function $f(x)$. If the function does not have any zeroes, or a double zero for $x > 0$, then according to Lemma (2.1) with $\lambda = 0$ there will not be any limit cycles for $x > 0$. A necessary condition to have these two simple zeroes is $-\frac{b}{K} + c > 0$. Otherwise, the function would be negative for all $x > 0$.

The equation determining the singularities of the system is given by $g(x) = 0$. This leads to a quadratic equation in x : $M(x) \equiv \mu a + \mu b x + \sigma x^2 = 0$. This equation can only have a positive zero if $\sigma < 0$, which will be unique. \square

We need to take the following three relative configurations of these zeroes into consideration.

Definition 3.1. Distinguish the following three cases for system (3.1).

- **Case (i).** $0 < x_f^{(1)} < x_f^{(2)} < x_g$.
- **Case (ii).** $0 < x_f^{(1)} < x_g < x_f^{(2)}$.
- **Case (iii).** $0 < x_g < x_f^{(1)} < x_f^{(2)}$.

In principle, we should also impose $x < K$, but for our purposes, this condition will not be needed, and we omit it to simplify the proof. In Figure 1, the three relative positions of the zeroes of the functions $f(x)$ and $g(x)$ are shown. For Case (i) and Case (iii), the singularity is stable for $f(x_g) > 0$ in those configurations. This is the case considered in [15], where it was proved that no limit cycles occur. In the next section, we will give a simpler proof using Lemma 2.1.

For Case (ii), the singularity is unstable and because of the boundedness of the system (see [15], where this was proved), at least one (stable) limit cycle will occur. Proving the uniqueness of the limit cycles in this case is the focal point of this paper.

4. Non-existence of limit cycles: the case of a stable singularity

For Case (i) $0 < x_f^{(1)} < x_f^{(2)} < x_g$ and Case (iii) $0 < x_g < x_f^{(1)} < x_f^{(2)}$ in Definition 3.1, we will show that condition (ii) of Lemma 2.1 is satisfied, i.e., we will show the

existence of a constant λ such that $Z_\lambda(x)$ in (3.3) has a fixed sign for $x > 0$.

Proposition 4.1. *System (1.1) has no limit cycles in Case (i) of Definition 3.1.*

Proof. We construct the λ of condition (ii) in Lemma 2.1. First, we find a value of λ_1 such that $Z_{\lambda_1}(x)$ has a double zero $x = \bar{x}$ in the interval $x_f^{(1)} < x < x_f^{(2)}$. Such a λ_1 should satisfy

$$\begin{aligned} f(\bar{x}) &= \lambda_1 g(\bar{x}), \\ f'(\bar{x}) &= \lambda_1 g'(\bar{x}). \end{aligned} \quad (4.1)$$

Eliminating λ_1 from the two equations gives the following condition on \bar{x} :

$$W(\bar{x}) \equiv \frac{f'(\bar{x})}{f(\bar{x})} - \frac{g'(\bar{x})}{g(\bar{x})} = 0.$$

The function $W(x)$ has the following properties

$$\begin{aligned} \lim_{x \downarrow x_f^{(1)}} W(x) &< -\infty, \\ \lim_{x \uparrow x_f^{(2)}} W(x) &> \infty. \end{aligned} \quad (4.2)$$

Since $W(x)$ is continuous on the interval $x_f^{(1)} < x < x_f^{(2)}$ (the denominator $g(x)$ cannot be zero, because x_g lies outside this interval), it follows that the function has a zero \bar{x} . For this zero, the system of equations (4.1) has a solution with $\lambda_1 = \frac{\tilde{f}(\bar{x})}{\tilde{g}(\bar{x})} > 0$.

The numerator of the function $Z_{\lambda_1}(x)$ is a cubic function in x , for which we know $Z_{\lambda_1}(0) < 0$, because $\tilde{f}(0) < 0$, $\tilde{g}(0) > 0$ and $\lambda_1 > 0$. Moreover, for large negative x the cubic term in $f(x)$ will dominate, and we have

$$\lim_{x \rightarrow -\infty} Z_{\lambda_1}(x) = \infty.$$

Therefore, $Z_{\lambda_1}(x)$ has another zero $x^* < 0$.

From this construction, we find that $Z_{\lambda_1}(x)$ has a double zero \bar{x} in the interval $x_f^{(1)} < x < x_f^{(2)}$ and a zero $x^* < 0$. Since the cubic function cannot have any other zeroes, we must have $Z_{\lambda_1}(x) < 0$ for $x \neq \bar{x}$ and $x > 0$. We change λ_1 into $\lambda = \lambda_1 + \epsilon$, where $\epsilon > 0$ is small enough such that the double zero at $x = \bar{x}$ disappears, and no other zeroes are introduced. For this λ , the function $Z_\lambda(x) < 0$ for all $x > 0$. According to Lemma 2.1 condition (ii) is satisfied and the system does not have limit cycles. See Figure 2 for the geometrical interpretation of this proof. \square

The same procedure also works for Case (iii) of Definition 3.1:

Proposition 4.2. *System (1.1) has no limit cycles in Case (iii) of Definition 3.1.*

Proof. The proof exactly follows the same construction as in the proof of Proposition 4.1. First, a double zero $x = \bar{x}$ for $Z_{\lambda_1}(x)$ is created on the interval $x_f^{(1)} < x < x_f^{(2)}$ with in this case $\lambda_1 < 0$. Due to the fact that $Z_{\lambda_1}(0) < 0$ and $\lim_{x \rightarrow -\infty} Z_{\lambda_1}(x) = \infty$, another zero needs to exist for $x < 0$. The cubic nature of the numerator of $Z_{\lambda_1}(x)$ then ensures that for $x > 0$ it is always negative except at the double zero $x = \bar{x}$. Then, changing λ_1 into $\lambda = \lambda_1 - \epsilon$ with $\epsilon > 0$ gives a function $Z_\lambda(x)$,

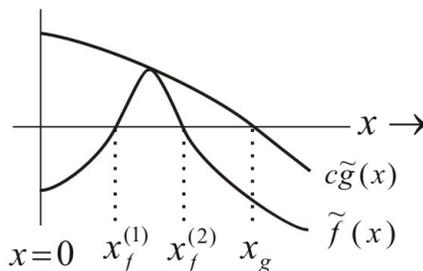


Figure 2. Construction of a constant λ such that $Z_\lambda(x)$ has a fixed sign for Case (i) of Definition 3.1.

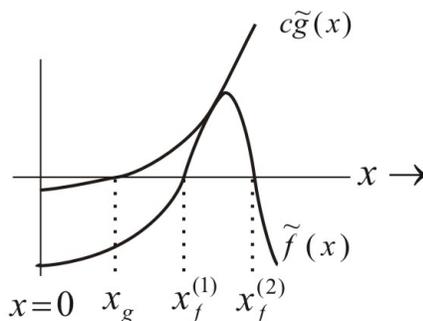


Figure 3. Construction of a constant λ such that $Z_\lambda(x)$ has a fixed sign for Case (iii) of Definition 3.1.

which is negative for all $x > 0$. According to Lemma 2.1, with condition (ii) satisfied, the system does not have limit cycles, completing the proof. The geometrical interpretation of this case is shown in Figure 3. \square

The two propositions of this section are combined showing (see [15] for another proof):

Theorem 4.1. *System (1.1) has no limit cycles, when the singularity in the first quadrant is locally stable.*

5. Uniqueness of limit cycles: the case of an unstable singularity

For Case (ii) $0 < x_f^{(1)} < x_g < x_f^{(2)}$ in Definition 3.1, we need to consider three possible configurations for the limit cycle. Since there are two simple positive zeroes of $f(x)$, a limit cycle can either cross both vertical lines where $f(x) = 0$ or cross only one vertical line.

Definition 5.1. There are three possible limit cycle configurations in system (1.1).

- **Case I.** The limit cycle crosses both lines $x = x_f^{(1)}$ and $x = x_f^{(2)}$.
- **Case II.** The limit cycle only crosses $x = x_f^{(2)}$ but not $x = x_f^{(1)}$.
- **Case III.** The limit cycle only crosses $x = x_f^{(1)}$ but not $x = x_f^{(2)}$.

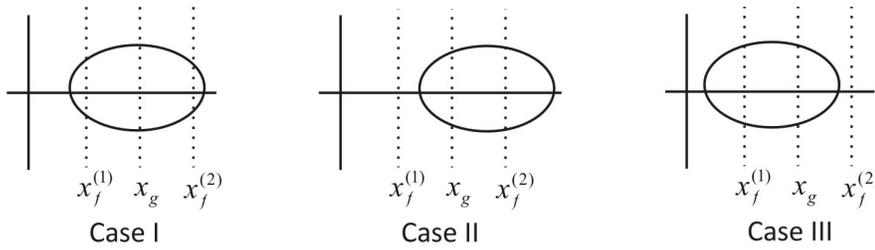


Figure 4. The three possible configurations for a limit cycle in system (3.1) of Definition 5.1

The three cases are shown in Figure 4. For each case, we will apply a different uniqueness theorem. The first question is on which intervals for $x > 0$ the function $\frac{f(x)}{g(x)}$ is monotonically decreasing, which is the critical condition in the application of the uniqueness theorems.

Lemma 5.1. For Case (ii) $0 < x_f^{(1)} < x_g < x_f^{(2)}$ in Definition 3.1, the function $\frac{f(x)}{g(x)}$ satisfies

$$\frac{d}{dx} \frac{f(x)}{g(x)} < 0 \quad \text{for } 0 < x < x_g \quad \text{and} \quad x > x_f^{(2)}.$$

Proof. The auxiliary function $U_\lambda(x) = r(-\frac{2cx^3}{K} + (-\frac{b}{K} + c)x^2 - a) - \lambda(-\sigma x^2 - \mu bx - \mu a) \equiv \tilde{f}(x) - \lambda \tilde{g}(x)$ as defined in (3.3) corresponds to the function determining the intersections of the graph of $y = \frac{f(x)}{g(x)}$ with horizontal lines $y = \lambda$. The result of the lemma follows, if we prove that $U_\lambda(x)$ only has simple zeroes for all $\lambda \in \mathbb{R}$ on the intervals $0 < x < x_g$ and $x > x_f^{(2)}$. The following properties follow from an elementary calculation.

- i) $U_\lambda(0) = a(-1 + \lambda\mu)$.
- ii) $U'_\lambda(0) = \lambda\mu b$.
- iii) $U_\lambda(x_g) = -\frac{2cx_g^3}{K} + (-\frac{b}{K} + c)x_g^2 - a > 0$.
- iv) $\lim_{x \rightarrow \infty} U_\lambda(x) = -\infty$.
- v) $\lim_{x \rightarrow -\infty} U_\lambda(x) = \infty$.

Property (iii) follows from the fact that in Case (ii), the singularity at $x = x_g$ lies between the two zeroes of $f(x)$.

Since $0 < x_f^{(1)} < x_g < x_f^{(2)}$, it is easy to see that $f(x) < 0$ (> 0), for $x < x_f^{(1)}$ and $x > x_f^{(2)}$ ($x_f^{(1)} < x < x > x_f^{(2)}$). Moreover, $g(x) < 0$ (> 0), for $0 < x < x_g$ ($x > x_g$).

It follows that $U_\lambda(x)$ does not have zeroes for $\lambda \leq 0$, $0 < x < x_f^{(1)}$ and $x_g < x < x_f^{(2)}$ ($\lambda \geq 0$, $x_f^{(1)} < x < x_g$ and $x > x_f^{(2)}$).

First, we consider the case $\lambda < 0$. For the cubic function $U_\lambda(x)$, it holds true that $U_\lambda(x_f^{(1)}) = -\lambda(-\sigma(x_f^{(1)})^2 - \mu bx_f^{(1)} - \mu a) < 0$ and $U_\lambda(x_f^{(2)}) = -\lambda((-\sigma(x_f^{(2)})^2 - \mu bx_f^{(2)} - \mu a)) > 0$, for $0 < x_f^{(1)} < x_g < x_f^{(2)}$. These results lead to sign changes in the function $U_\lambda(x)$ for each $\lambda < 0$.

Property (v). $U_\lambda(-\infty) = \infty$,

- Property (i). $U_\lambda(0) < 0, U_\lambda(x_f^{(1)}) < 0, U_\lambda(x_g) > 0, U_\lambda(x_f^{(2)}) > 0,$
- Property (iv). $U_\lambda(\infty) = -\infty.$

This shows that $U_\lambda(x)$ has a simple zero for $x < 0, x_f^{(1)} < x < x_g, x > x_f^{(2)},$ for all $\lambda < 0.$ Since $U_\lambda(x)$ does not have a zero for $\lambda \geq 0,$ in this case, we have proved that $U_\lambda(x)$ only has simple zeroes for all $\lambda \in \mathbb{R}$ on the intervals $x_f^{(1)} < x < x_g$ and $x > x_f^{(2)}.$ Therefore, $\frac{d}{dx} \frac{f(x)}{g(x)} < 0$ on those intervals. The minus sign follows from property (ii) above and the behaviour of the function for large $x.$

Next, to complete the proof, we consider the interval $0 < x < x_f^{(1)}.$ Here, $U_\lambda(x)$ can only have zeroes for $\lambda > 0.$ For $0 < \lambda < \frac{1}{\mu},$ property (i) says $U_\lambda(0) > 0,$ while $U_\lambda(x_f^{(1)}) < 0.$ Therefore, there is a zero on this interval. Since $U_\lambda(-\infty) = \infty$ and $U_\lambda(\infty) = \infty,$ there are two additional zeroes outside this interval, which implies that the zero in the interval $0 < x < x_f^{(1)}$ is simple due to the cubic nature of $U_\lambda(x).$ For $\lambda \geq \frac{1}{\mu},$ the function $U_\lambda(x)$ cannot have a zero $\in 0 < x < x_f^{(1)}.$ The case of $\lambda = \frac{1}{\mu}$ is a limiting case of $0 < \lambda < \frac{1}{\mu},$ where the unique zero in the interval $0 < x < x_f^{(1)}$ has been moved to $x = 0.$ Therefore, for $\lambda = \frac{1}{\mu},$ it is true that $U_\lambda(x) > 0,$ for all $0 < x < x_f^{(1)}.$ Since $\tilde{g}(x) < 0$ on this interval, we get $U_\lambda(x) = U_{\frac{1}{\mu}}(x) - (\lambda - \frac{1}{\mu})\tilde{g}(x) > 0$ for $\lambda \geq \frac{1}{\mu},$ which completes the proof. □

A consequence of this lemma is that $\frac{f(x)}{g(x)} < \frac{f(0)}{g(0)} = \frac{1}{\mu}$ on the interval $0 < x < x_g.$

Corollary 5.1. *The system of equations*

$$\begin{aligned} F(x_1) &= F(x_2), \\ \frac{f(x_1)}{g(x_1)} &= \frac{f(x_2)}{g(x_2)}, \end{aligned}$$

in condition (iv) of theorem 2.2 can only have solutions for those $x_2 > x_g$ such that $\frac{f(x_2)}{g(x_2)} < \frac{1}{\mu}.$

This observation is crucial, because it will imply that the system has at most one non-trivial solution as we will prove below.

With this lemma two of the three cases for the limit cycle configurations in Definition 5.1 can be resolved.

Proposition 5.1. *System (3.1) has at most one limit cycle in Case (i) of Definition 5.1 intersecting both zeroes of $f(x)$ of (3.2). When it exists, it is stable and hyperbolic.*

Proof. The first three conditions of Theorem 2.1 are trivially satisfied according to (3.2) and Lemma 3.1, taking $x_- = 0$ and $x_+ = \infty.$ Condition (iv) is satisfied according to Lemma 5.1. □

Proposition 5.2. *System (3.1) has at most one limit cycle in Case (ii) of Definition 5.1 intersecting only the zero $x_f^{(2)} > x_g$ of $f(x)$ of (3.2) (and not the zero $x_f^{(1)} < x_g$). When it exists, it is stable and hyperbolic.*

Proof. Again, the first three conditions of Theorem 2.3 are trivially satisfied according to (3.2) and Lemma 3.1 taking $x_- = 0$ and $x_+ = \infty.$ Condition (iv) is satisfied as well according to Lemma 5.1. □

The remaining Case (iii) in Definition 5.1 where the limit cycle only intersects the zero $x_f^{(1)} < x_g$ requires more attention, because it is not clear whether the function $\frac{f(x)}{g(x)}$ is monotonically decreasing on the interval $x_g < x < x_f^{(2)}$, which would be necessary for applying Theorem 2.3. Therefore, we resort to the stronger Theorem 2.2 which only requires the function to be monotonic on $0 < x < x_f^{(1)}$. This is true according to Lemma 5.1.

Proposition 5.3. *System (3.1) has at most one limit cycle in Case (iii) of Definition 3.1 intersecting only the zero $x_f^{(1)} < x_g$ of $f(x)$ of (3.2) (and not the zero $x_f^{(2)} > x_g$). When it exists, it is stable and hyperbolic.*

Proof. Again, the first three conditions of Theorem 2.2 are trivially satisfied according to (3.2) and Lemma 3.1 taking $x_- = 0, x_+ = \infty$. Condition (v) is satisfied as well according to Lemma 5.1. It remains to prove that the system of equations in condition (iv) has at most one non-trivial solution.

Since Corollary 5.1 states that only those x_2 need to be considered for which $\frac{f(x_2)}{g(x_2)} < \frac{1}{\mu}$, because only in that case, there exists a $0 < x_1 < x_f$ such that $\frac{f(x_1)}{g(x_1)} = \frac{f(x_2)}{g(x_2)}$. In the case $0 < x_1 < x_f^{(1)}$, according to Lemma 5.1, the function $\frac{f(x_1)}{g(x_1)}$ is monotonically decreasing, i.e., $\frac{f(x_1)}{g(x_1)} = C$ has exactly one solution and $0 < C < \frac{1}{\mu}$. The horizontal line $y = C$ intersects the graph of $y = \frac{f(x)}{g(x)}$ in the two points $x = x_1$ and $x = x_2$ by construction, where $x_g < x_2 < x_f^{(2)}$. It means that the function $U_\lambda(x)$ as defined in the proof of Lemma 5.1, for $\lambda = C$ has at least two zeroes, x_1 and x_2 . On the interval $x_g < x_2 < x_f^{(2)}$, it is easy to see that the number of zeroes of $U_C(x)$ is odd (counting multiplicities). This is for $U_C(x_g) > 0$ (property (ii) in the proof of Lemma 5.1) and $U_C(x_f^{(2)}) = -Cg(x_f^{(2)}) < 0$. Therefore, the zero at $x = x_2$ is a unique simple zero on this interval, because the cubic function $U_C(x)$ cannot have more than 3 zeroes.

It follows that for those x_2 such that $\frac{f(x_1)}{g(x_1)} = \frac{f(x_2)}{g(x_2)}$, $\frac{d}{dx_2} \frac{f(x_2)}{g(x_2)} < 0$. The curve $x_2 = \gamma_{f/g}(x_1)$ is a monotonically increasing function, for $\frac{dx_2}{dx_1} = \frac{\frac{d}{dx_1} \frac{f(x_1)}{g(x_1)}}{\frac{d}{dx_2} \frac{f(x_2)}{g(x_2)}} > 0$. The other equation $F(x_1) = F(x_2)$ defines a curve $x_2 = \gamma_F(x_1)$, for which $\frac{dx_2}{dx_1} = \frac{\frac{d}{dx_1} F(x_1)}{\frac{d}{dx_2} F(x_2)} = \frac{f(x_1)}{f(x_2)} < 0$. The two curves $x_2 = \gamma_{f/g}(x_1)$ and $x_2 = \gamma_F(x_1)$ have opposite slopes, and they can have at most one intersection proving that the system of equations has at most one non-trivial solution. Condition (iv) of Theorem 2.2 is satisfied, which shows that at most one limit cycle can occur. \square

The three results of this section are combined to show the following.

Theorem 5.1. *System (1.1) has exactly one limit cycle, which is stable and hyperbolic, when the singularity in the first quadrant is locally unstable.*

Proof. The three propositions 5.1, 5.2 and 5.3 state that the limit cycle of each type is unique and stable. However, since adjacent limit cycles cannot have the same stability, only one limit cycle can exist which is stable. It is not a priori clear, which of the three types will occur. The existence of the limit cycle follows from the fact that system (1.1) is bounded and the singularity is unstable. Since there are no other attracting singularities in the first quadrant, the Poincaré-Bendixson theorem shows the existence of the limit cycle. See Figure 5 where a numerical example of

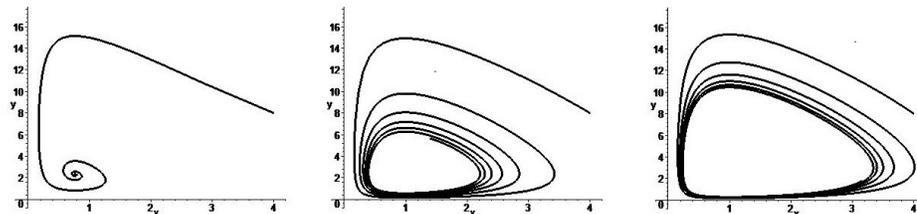


Figure 5. Three numerical examples of system (1.1). In the first case, the singularity is globally asymptotically stable without limit cycles. The parameter values are $\beta = 4, \mu = 1, a = 1, b = 1, c = 1, K = 3$ and $r = 1$. In the second case and third case, the singularity is locally unstable, and a unique limit cycle occurs according to Theorem 5.1. The parameter values are $\beta = 5, \mu = 2, a = 0.5, b = 1, c = 1, K = 7$ and $r = 1$ for case 2 and the same for case 3 except that $K = 10$.

the limit cycle is presented. □

6. Discussion

For small prey densities, the functional response function in (1.1) behaves as a quadratic function which is a restriction not imposed by most papers on predator-prey systems. To impose a sigmoid shape, it is not necessary to restrict the functional response to this quadratic behaviour. To illustrate this idea, we can consider the more general sigmoid functional response

$$p(x) = \frac{dx + x^2}{a + bx + cx^2}, \tag{6.1}$$

with $d > 0$.

The functional form in system (6.1) will have an sigmoidal functional form, when the parameter d is positive and not too large: a straightforward computation shows $p''(0) = \frac{2(a-db)}{a^2}$. It means that if d is not too large, the functional response remains sigmoidal. It can be viewed as a mixture of the sigmoid functional response in [15] and a Monod-Haldane functional response. In this paper, we proved the uniqueness of the limit cycle when $d = 0$ in (6.1), but it would be interesting to see how many limit cycles the more general system with $d > 0$ would have. We expect this system to have two limit cycles for certain values of the parameters. This is a question to be resolved in future research.

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