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Elemental access to limit cycle existence in Biomath education

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This paper originated from the desire to develop elementary calculus based tools to empower students, not necessarily with a strong mathematical background, to test predator-prey related models for boundedness of solutions and for the existence of limit cycles. There are several well-known methods available to prove, or disprove, the existence of bounded solutions to systems of differential equations. These methods rely on Liénard's theorem or using Dulac or Lyaponov functions. The level of mathematics required in the study of differential equations is not addressed in the courses presented on the first year level, and students in biology, ecology, economics and other fields are often not suitably equipped to perform these advanced techniques. The conditions under which a unique limit cycle exists in predator-prey systems is considered a primary problem in mathematical ecology [1, 2]. A great deal of mathematical effort has gone into trying to establish simple, yet general, theorems which will allow one to decide

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whether a given set of nonlinear equations has a limit cycle or not [3]. We introduce a method to first determine the boundedness of solution trajectories in such a way that the transformation to a Liénard system or the use of a Dulac function can be avoided. Once boundedness of trajectories has been established, the nature of the equilibrium points reduces to simple eigenvalue analysis. The Elemental Limit Cycle method (ELC) provides elementary criteria to evaluate the nature of the pivotal functions of a system which will indicate boundedness and may be applicable to more general models.

1 Introduction

Dynamical systems theory originated with the work on celestial mechanics by Poincaré in 1899 and is based on analysis, geometry and topology . Poincaré laid the foundations for qualitative analysis of nonlinear differential equations, and began to develop a coherent set of mathematical tools for their study.

The dynamics of various interacting species may, in general, be modeled by such a nonlinear set of differential equation. There has been a surge of interest in developing and analyzing models of interacting species in ecosystems, with specific interest in investigating the existence of limit cycles in systems describing the dynamics of these species [4]. The original Lotka-Volterra model does not possess any limit cycles and for this reason has been labeled as ecologically unstable. This model has subsequently been modified to take disturbances into consideration that allow populations to return to their original numbers.

In the search for population models that possess limit cycles we will focus on the existence of bounded solutions. A system of differential equations with bounded solutions has the potential for periodic solutions which, in turn, suggests stability. Ecologically this means that the species coexist and that extinctions do not occur. In the case of the system possessing a stable limit cycle it provides a satisfying explanation for those animal communities in which populations are observed to oscillate in a rather reproducible periodic manner.

Several well-known methods are available to prove or disprove the existence of bounded solutions. Many of these techniques are perceived as mathematically challenging, yet often students in biological sciences and economics are equipped with only one semester of mathematics [5, 6]. The challenges that future biologists faces dictate a change in the way we prepare undergraduates who wish to pursue a career in the life sciences. The 21st-century challenges involve complex systems that no single discipline can fully address [7]. Despite this, most colleges and universities do not require an in depth knowledge of calculus from their biology majors [8].

A sound knowledge of calculus and differential equations is required when attempting to investigate and interpret the results of the models concerned with population dynamics. Researchers in ecology and other fields may need to transform a system of differential equations into a Liénard system, for which there are no set rules as to which transformation should be used. Similarly, if Dulac or Lyaponov functions are used, there are no systematic procedures on how these functions should be chosen. The approach suggested here to determine whether or not a model has periodic solutions is the application of Poincaré-Bendixson theory which, according to Zill and Cullen [9], is an advanced result that describes the long-term behaviour of a bounded solution. This theorem relies on the existence of an invariant region R, which is a region that, whenever a trajectory $(x(t), y(t))$ enters this region, it remains in R as $t \to \infty$. Determining the existence of such a region is considered to be extremely difficult and therefore the problem of boundedness of solutions of nonlinear systems of differential equations is nontrivial. Once the existence of an invariant region has been established and thus the solution trajectories are bounded, eigenvalue analysis can be used to determine the nature of the equilibrium points. The Poincaré-Bendixon Theorem [9] predicts that if a single equilibrium point exists within this bounded region, then it is either an attracting spiral point, suggesting a stable population pair, or an unstable node, resulting in a unique limit cycle. Our purpose in this paper is therefore to propose a method or technique which greatly reduces the mathematical difficulties encountered when investigating the boundedness of trajectories of predator-prey models, called the Elemental Limit Cycle method (ELC). The technique replaces the need to deal with complex Liénard systems, Dulac and Lyaponov functions and hence the required mathematics becomes accessible to researchers in a wide range of disciplines.

In the following two sections models suggested by Kuang and Freedman [10] and Huang and Zhu [11] are discussed with special cases. Conditions ensuring existence of limit cycles are explored and Mathematica is used to illustrate the findings. The methods used by these authors to prove boundedness of solutions are reviewed and then compared to the ease with which the ELC can be applied in order to reach the same results.

2 The Kuang and Freedman Model

This section deals primarily with the boundedness of solutions of a class of Gause-type predator-prey models. The model proposed by Kuang and Freedman [10], can have a limit cycle and is useful in illustrating the development of the ELC method. Kuang and Freedman consider a Gause-type predator-prey model of the form

$$\begin{aligned} \dot{x} &= xg(x) - \xi(y)p(x), \qquad & x(0) \geq 0 \\ \dot{y} &= \eta(y)[-\gamma + q(x)], \qquad & y(0) \geq 0 \end{aligned} \tag{1}$$

where $x(t)$ denotes the number of prey and $y(t)$ denotes the number of predators at given time t. Furthermore g, ξ, p, η and q are continuous with piecewise continuous first derivatives for $t \geq 0$. The usual predator-prey assumptions as discussed by Freedman [12] are applicable. They transform System (1) into a generalized Liénard system, which then proves that the system has bounded solutions. A theorem by Cherkas and Zhilevich [13] on the existence of limit cycles in a generalized Liénard system and a theorem by Zhang [14] on the uniqueness of these limit cycles are applied by Kuang and Freedman to show that a unique limit cycle exists.

2.1 Assumptions applying to the Kuang and Freedman Model

We now introduce an alternative method of proving that the trajectories of System (1) are bounded and therefore that an invariant region exists. It should be noted that similar, but more complex, arguments have been used by Chen et al. [15] and Huang [16]. The assumptions needed to simplify our method are similar to the assumptions of Kuang and Freedman and are reasonable for a predator-prey model.

For System (1) the function $g(x)$ represents a logistic type or alternative growth function for the prey x which is non-negative and has a maximum, G, over an interval $[0, K]$. A few possible functions for $g(x)$ is illustrated in Figure 1.

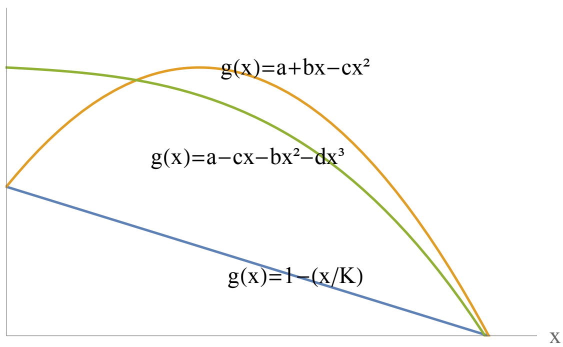

Figure 1: The positive quasi-logistic function $g(x)$)

The function $\xi(y)$ represents the predation rate of the predator population y on the prey population x. Suppose that it is bounded by two linear functions sy and Sy, where s is the minimal predator efficiency and S is the maximal predator efficiency. Therefore $sy \leq \xi(y) \leq Sy$.

The functions $p(x)$ and $q(x)$ are Holling type I, II or III prey-dependent functional responses, or any other function that displays the same bounded characteristics. Each of these functions is bounded above by some constant, say a_1 and a_2 respectively. It will be argued below that there is no loss of generality to assume that x is always less than K, therefore $p(x)$ and $q(x)$ are bounded below by the linear function $p(K)x/K$ and $q(K)x/K$ respectively. The positioning of the function $p(x)$ is depicted in Figure 2.

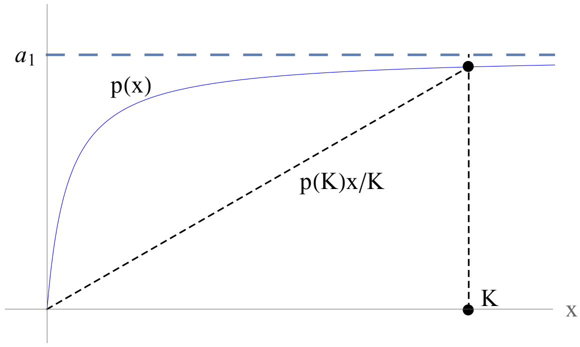

Figure 2: A possible graph of $p(x)$

Thus $p(K)x/K \leq p(x) \leq a_1$ and similarly $q(K)x/K \leq q(x) \leq a_2$ for all x in the interval $[0, K]$. The product $-\gamma\eta(y)$ is a decreasing function representing the mortality rate of the predator in the absence of prey. Assume that there are positive constants n and N so that $-Ny \leq -\gamma\eta(y) \leq -ny$ as depicted in Figure 3.
From the discussion above and for reference purposes the assumptions are stated here as (H1) to (H3).

(H1): $g(0) > 0$ and there exists a $K > 0$ so that $g(x) > 0$ over the interval $[0, K)$, $g(K) = 0$, and $g(x) < 0$ if $x > K$. Let G denote the maximum value of $g(x)$ over the interval $[0, K]$

(H2): $p(0) = q(0) = 0$ and $p'(x) > 0$ and $q'(x) > 0$ for all $x > 0$. There exist positive numbers a_1 and a_2 so that $p(K)x/K \leq p(x) \leq a_1$ and $q(K)x/K \leq q(x) \leq a_2$ for all x in the interval $[0, K]$.

(H3): $\xi(0) = \eta(0) = 0$ and $\xi'(y) > 0$ and $\eta'(y) > 0$ for all $y > 0$. There exist positive numbers s and S so that $sy \leq \xi(y) \leq Sy$ for all $y \geq 0$.

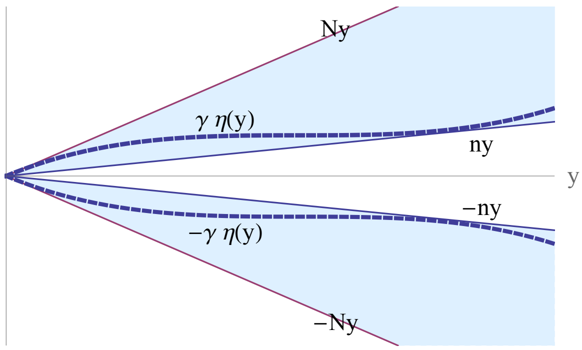

Figure 3: The decreasing function $-\gamma\eta(x)$ representing the mortality rate of the predator in the absence of prey.

There exist positive numbers n and N so that $-Ny \leq -\gamma\eta(y) \leq -ny$ for all $y \geq 0$.

2.2 Boundedness of $x(t)$ and $y(t)$ for the Kuang and Freedman model

We introduce a new function $\omega(x, y)$ and show that $\omega(x, y)$ has bounded solutions. It should be obvious that the simplistic choice of $\omega = x + y$ used below can be modified to accommodate different models.

First note that if $x(0) \geq K$, then $g(x) \leq 0$ resulting in $\dot{x} < 0$. Therefore $x(t)$ is decreasing and will continue to decrease until $x(t)$ is less than K. The interaction between $xg(x)$ and $p(x)\xi(y)$ may permit $\dot{x}$ to change sign so that $x(t)$ starts increasing. However, since $\dot{x}$ is negative at K, $x(t)$ can now never become as large as K again. Hence $x(t)$ is bounded by K as $t \to \infty$. Therefore without loss of generality, it can be assumed that $0 < x(t) < K$ as $t \to \infty$, as depicted in Figure 4.

Given the assumptions (H1) to (H3), we show that the solutions $x(t)$ and $y(t)$ of System (1) are bounded as $t \to \infty$.

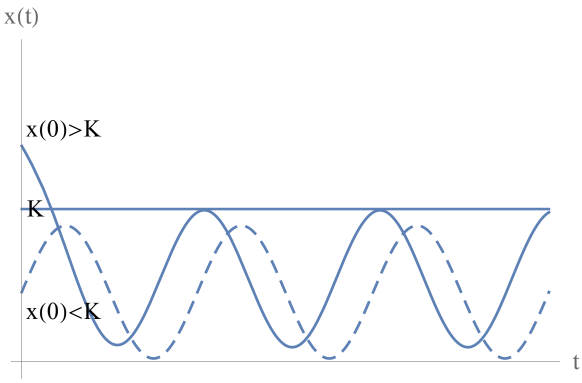

Figure 4: The solution trajectory $x(t)$ remains between 0 and K as $t \to \infty$.

Suppose $x(t)$ and $y(t)$ are solutions of System (1). Define $\omega(t, x, y) = x(t) + y(t)$ then

$$\dot{\omega} = xg(x) - \xi(y)p(x) + \eta(y)[-\gamma + q(x)]$$
$$\dot{\omega} \leq KG - \frac{p(K)x}{K}sy - \gamma\eta(y) + a_2\eta(y)$$

and since $0 < x < K$ and $ny \leq \gamma\eta(y) \leq Ny$,

$$\dot{\omega} \leq KG - ny + a_2\frac{Ny}{\gamma}.$$

Adding and subtracting x and factoring, it follows that

$$\dot{\omega} \leq KG + K - y\left(n - a_2\frac{N}{\gamma}\right) - x$$
$$\dot{\omega} \leq KG + K - \min\left\{\left(n - a_2\frac{N}{\gamma}\right), 1\right\}(x + y)$$

Let $A = KG + K$ and $B = \min\{(n - a_2N/\gamma), 1\}$, then $\dot{\omega} + B\omega \leq A$. Applying the positive integrating factor e^{Bt} and solving the integral yields

$$e^{Bt}\omega \leq (A/B) + c,$$

where c is a constant of integration. Therefore

$$\omega \leq A/B + ce^{-Bt}.$$

Now $\omega(t)$ is bounded as $t \to \infty$ and since $x(t)$ is bounded, $y(t)$ is bounded as well.

2.3 Eigenvalue analysis for the Kuang and Freedman model

Eigenvalue analysis will now be applied to determine the nature of the roots of the characteristic equation, which will provide information on the long term behaviour of the system.

It is convenient to use the signs of the determinant and trace of the Jacobian matrix. In particular, if both the determinant and the trace of the Jacobian matrix are positive then the equilibrium point $E^*(x^*, y^*)$ is unstable. It is easily shown that the determinant and the trace of the Jacobian matrix for System (1) is given by

$$\Delta = p(x^*)q'(x^*)\eta(y^*)\xi'(y^*) \tag{2}$$

and

$$\tau = J(x^*) \tag{3}$$

where

$$J(x^*) = p(x)\frac{d}{dx}\left(\frac{xg(x)}{p(x)}\right) \tag{4}$$

where $x = x^*$ and we may therefore conclude that if both $\Delta > 0$ and $\tau > 0$ then the equilibrium $E^*(x^*, y^*)$ is unstable and a limit cycle exists. In the following example the respective conditions for the existence, uniqueness and instability of the equilibrium in the population quadrant is stated, followed by a numerical and graphical representation of the results.

2.4 Wang and Sun model

The Wang and Sun model [17] is a special case of the Kuang and Freedman [10] model supporting a Holling type -$(n + 1)$ functional response:

$$
\begin{aligned}
\dot{x} &= \gamma x(1 - h(x)) - \frac{x^n y}{(a + x^n)} \\
\dot{y} &= y[-\beta + \frac{\mu x^n}{(a + x^n)}
\end{aligned}
\tag{5}
$$

with an added condition namely

$$
h(0) = 0, h^{(k)}(x) \geq 0, 1 \leq k \leq (n + 3) \tag{6}
$$

for any $n \in N^+$ and all $x \in R^+$ where N^+ and R^+ are the integer set and positive real number set respectively.

Wang and Sun use a Dulac function, which is deemed "very technical and difficult", as well as a transformation into a generalized Liénard system to prove that, under certain conditions, this model possesses a unique limit cycle. The difficulty in finding a suitable Dulac function is due to the fact that there are no set guidelines available on how to choose such a function.

The main result achieved by Wang and Sun [17] states that under Assumption (6), the System (5) has a unique limit cycle if and only if its only positive equilibrium is unstable, that is, if $P_0 > 0$ where

$$
P_0 = \gamma[(1-n)a-(1-n)ah(x_0)+x_0^n-x_0^{n+1}h'(x_0)-ax_0h'(x_0)-x_0^n h(x_0)] \tag{7}
$$

The expression for P_0 originates from the complicated choice of a Dulac function. Since System (5) is a special case of System (1) set

$$
\begin{array}{lll}
g(x) = \gamma(1 - h(x)) & p(x) = x^n/(a + x^n) & q(x) = \mu x^n/(a + x^n) \\
\xi(y) = y & \eta(y) = y & \gamma = \beta
\end{array}
$$

It is easily shown that the assumptions (H2) and (H3) are satisfied. The function $g(x) = \gamma(1 - h(x))$ is in functional form like a quasi-logistic equation. To satisfy the assumption (H1), it is reasonable to assume that $(1 - h(0)) > 0$ and there exists a $K > 0$ such that $(1 - h(x)) > 0$ if $0 \leq x \leq K, (1 - h(K)) = 0$ and $(1 - h(x)) < 0$ if $x > K$. If this is the case, it can then be concluded that the solutions of the Wang and Sun model are bounded. Furthermore System (5) has equilibrium points at $E_0(1, 0)$ and $E^*(x^*, y^*)$ of which the latter lies in the population quadrant with

$$x^* = \sqrt{\frac{\beta a}{\mu - \beta}}$$

and

$$y^* = \frac{-\sqrt{a}\gamma(\beta + a\beta - \mu)\mu}{\sqrt{\beta}(\mu - \beta)^{3/2}}$$

Substituting x^* and y^* into equations (2), (3) and (4) results in

$$J(x^*) = -\frac{(\gamma\mu^2 + 2\gamma\beta^2 - 3\gamma\mu\beta + 2a\gamma\beta^2 + a\gamma\mu\beta)}{\mu^2 - \mu\beta}$$

and for E^* to be unstable we require that

$$\Delta = \frac{-2\gamma\beta(\beta - \mu + a\beta)}{\mu} > 0$$

and

$$\tau = -\frac{(\mu^2 + 2\beta^2 - 3\mu\beta + 2a\beta^2 + a\mu\beta)}{\mu^2 - \mu\beta} > 0.$$

Let $h(x) = x^2$ and $n = 2$ satisfying Condition (6). Furthermore let $\gamma = 3, a = 0.05, \beta = 3$ and $\mu = 4 > 0$, so that the inequalities above are satisfied and System (5) becomes

$$\dot{x} = 3x(1 - x^2) - \frac{x^2 y}{0.05 + x^2}$$
$$\dot{y} = y\left[-3 + \frac{4x^2}{0.05 + x^2}\right].$$

The determinant $\Delta = 3.825$ and the trace $\tau = 0.375$ are both positive, so that the equilibrium point $(0.387, 1.317)$ is unstable and thus a limit

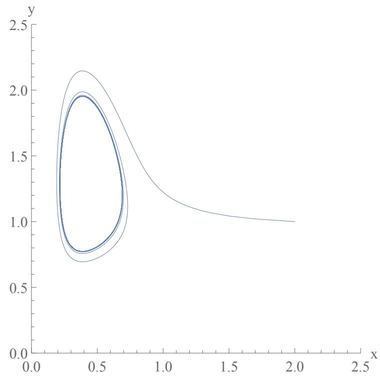

Figure 5: Limit cycle for the Wang and Sun model with initial value $(2, 1)$.

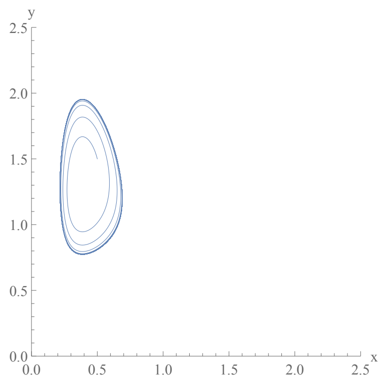

Figure 6: Limit cycle for the Wang and Sun model with initial value $(0.5, 1.5)$.

cycle exists. Also note that $P_0 = 0.075$, satisfying Condition (7) and confirming the result of Wang and Sun. Typical solution trajectories for the Wang and Sun model are shown in Figures 5 and 6.

This two-pronged approach can be applied to a diverse range of predator-prey models used in various fields of research. The same procedure can be used, making it possible to confirm the existence (or nonexistence) of an invariant region by identifying the various functions comprising the system. We require that one of the solutions is bounded. The boundedness of $x(t)$ is usually due to the density-dependent prey growth rate $g(x)$ in the form of a logistic growth function or any other form that curbs the growth rate of the prey so that Malthusian growth does not occur. If this behaviour can be identified, then the problem of proving boundedness is greatly simplified by the implementation of the ELC. The investigation of the existence of limit cycles in models is then greatly simplified to simple eigenvalue analysis. The use of a standardized test in terms of the determinant and the trace makes this even simpler. We demonstrate this on another well known model introduced by Huang and Zhu [11].

3 The Huang and Zhu model

Huang and Zhu [11] assume that in the following model the functions g, ξ, η, q, ϕ and ψ are defined such that existence, uniqueness and continuability for all $t \geq 0$ are satisfied for initial value problems.

$$\begin{aligned} \dot{x} &= \phi(x)(g(x) - \xi(y)) \\ \dot{y} &= \eta(y)[-\gamma + q(x) + \psi(y)] \end{aligned} \tag{8}$$

As before $x(0) > 0$ and $y(0) > 0$. In essence, the assumptions that Huang and Zhu place on the functions g, ξ, η, q, ϕ and ψ are the same as those used by Kuang and Freedman [10]. Obviously, $p(x)$ is no longer present and the addition of the functions $\phi(x)$ and $\psi(y)$ needs attention. Therefore, assumptions (H1) to (H3) must be modified:

(H1a): $g(0) > 0$ and there exists a $K > 0$ so that $g(x) > 0$ over the interval $[0, K)$, $g(K) = 0$, and $g(x) < 0$ if $x > K$. Let G denote the maximum value of $g(x)$ over the interval $[0, K]$.

(H1b): $\phi(0) = 0, \phi'(x) \geq 0$ and there exists positive constants r and R so that $rx \leq \phi(x) \leq Rx$ for all x in the interval $[0, K]$.

(H1c): $q(0) = 0$ and $q'(x) > 0$ for all $x > 0$. There exist a positive number a_2 so that $q(K)x/K \leq q(x) \leq a_2$ for all x in the interval $[0, K]$.

(H2a): $\psi(0) = 0$ and $\psi'(y) \leq 0$ for all $y > 0$.

By the Huang and Zhu assumptions the maximum value of $\psi(y)$ is H for all $y > 0$.

(H2b):$\xi(0) = \eta(0) = 0$ and $\xi'(y) > 0$ and $\eta'(y) > 0$ for all $y > 0$. There exist positive numbers s and S so that $sy \leq \xi(y) \leq Sy$ for all $y \geq 0$. There exist positive numbers n and N so that $-Ny \leq -\gamma\eta(y) \leq -ny$ for all $y \geq 0$.

Note that the parameter K in (H1b) is the same parameter as the one in (H1a). Finding the equilibrium points of System (8) results in one more condition:

Let $\eta(y)[-\gamma + q(x) + \psi(y)] = 0$.
If $\eta(y) = 0$ then $y = 0$ and therefore if $\phi(x)(g(x) - \xi(0)) = 0$ it leads to $\phi(x)g(x) = 0$ therefore $\phi(x) = 0 \Rightarrow x = 0$ or $g(x) = 0 \Rightarrow x = 0$ or $x = K$. All these options will lead to the extinction of one or both species.
So say $-\gamma + q(x) + \psi(y) = 0$ and let $\phi(x)(g(x) - \xi(y)) = 0$.
If $\phi(x) = 0$, then $x = 0$. Therefore $-\gamma + q(0) + \psi(y) = 0 \Rightarrow \psi(y) = \gamma$, which is not possible since $\psi(0) = 0$ and $\psi(y) \leq 0$. If $\phi(x) \neq 0$ then say that $g(x) - \xi(y) = 0$.
Therefore to ensure the existence of a unique equilibrium point $E^*(x^*, y^*)$ in the population quadrant we must therefore assume that: $g(x) - \xi(y) = 0$ and $x > 0$, and $q(x) + \psi(y) = \gamma$ is defined for all$x > 0$, $y \geq 0$ and $\gamma \geq 0$. This results in condition:

(H3a): There exists a $x^* \in (0, K)$ and $y^* \geq 0$ satisfying the equations $q(x) + \psi(y) = \gamma$ and $g(x) - \xi(y) = 0$ simultaneously.

Huang and Zhu prove, with eigenvalue analysis, that the equilibrium $E^*(x^*, y^*)$ will be unstable if three inequalities are satisfied. They then proceed to use phase portrait analysis to identify an annular region in the xy-plane, containing the point (x^*, y^*), where the solution trajectories of the System (8), either crosses from the exterior to the interior of the region, or stays on the boundary. This makes the annular region an invariant region so that the solutions are bounded. By the Poincaré-Bendixson theorem this implies that at least one limit cycle exists around the equilibrium point. They also prove that this limit cycle is unique. For a detailed discussion the reader is referred to Huang and Zhu [11].

3.1 Boundedness of $x(t)$ and $y(t)$ for the Huang and Zhu model

Using the method used in Section 2.2 we now prove the boundedness of the solutions of System (8) and once this has been done, the same results follow with regards to the existence of at least one limit cycle in the invariant region. As before, say $x(t)$ and $y(t)$ are solutions of System (8). As in the case of Kuang and Freedman in the previous section, it can be assumed that $x(t)$ is bounded, that is $0 < x(t) < K$ as t becomes large. Given the assumptions (H1a) to (H1c), (H2a) and (H2b), we show that the solutions $x(t)$ and $y(t)$ of System (8) are bounded as $t \to \infty$.

Define $\omega(t, x, y) = x(t) + y(t)$ then

$$\begin{aligned}
\dot{\omega} &= \dot{x} + \dot{y} \\
&= \phi(x)g(x) - \phi(x)\xi(y) + \eta(y)(-\gamma + q(x) + \psi(y)) \\
&\leq RxG - rxsy + \eta(y)(-\gamma + a_2 + H) \\
&\leq RKG + Ny(-\gamma + a_2 + H) + Nx - Nx \\
&\leq RKG + NK - Ny(\gamma - a_2 - H) - Nx \\
&\leq (RKG + NK) - N\min\{(\gamma - a_2 - H), 1\}(x + y) \\
&\leq A - B\omega
\end{aligned}$$

where $A = RKG + NK$ and $B = N\min\{(\gamma - a_2 - H), 1\}$.
Thus we have $\dot{\omega} + B\omega \leq A$ resulting in $\omega \leq A/B + ce^{-Bt}$ and if $t \to \infty$ then $\omega \leq A/B$ and assuming that $B > 0$ implies that ω is bounded and since $x(t)$ is bounded it follows that $y(t)$ is also bounded. This

once again proves the existence of an invariant region for the System (8) and once again eigenvalue analysis can be applied to determine the nature of the roots of the characteristic equation. This will provide the information needed to decide if the existence of a limit cycle is possible.

3.2 Eigenvalue analysis for the Huang and Zhu model

If it can be shown that a single, unstable, equilibrium point exists in the population quadrant then, by Poincaré-Bendixson Theory, there must exist at least one periodic solution which is a limit cycle [9]. By assumption (H3a) the equilibrium point $E^*(x^*, y^*)$ exists in the population quadrant and is unique.
We show that the equilibrium point $E^*(x^*, y^*)$ in the population quadrant is unstable if the following conditions are met:

$$\begin{aligned} g'(x^*)\psi'(y^*) + q'(x^*)\xi'(y^*) &> 0 \\ \phi(x^*)g'(x^*) + \eta(y^*)\psi'(y^*) &> 0 \\ g(x^*) &> 0 \end{aligned} \tag{9}$$

The Jacobian of System (8) is given by

$$J(x,y) = \begin{bmatrix} \phi'(x)(g(x) - \xi(y)) + \phi(x)g'(x) & -\phi(x)\xi'(y) \\ \eta(y)q'(x) & \eta'(y)(-\gamma + q(x) + \psi(y)) + \eta(y)\psi'(y) \end{bmatrix}$$

and since by assumption (H3a)
$g(x^*) - \xi(y^*) = 0$ and $q(x^*) + \psi(y^*) = \gamma$

$$J(x^*, y^*) = \begin{bmatrix} \phi(x^*)g'(x^*) & -\phi(x^*)\xi'(y^*) \\ \eta(y^*)q'(x^*) & \eta(y^*)\psi'(y^*) \end{bmatrix}.$$

For E^* to be unstable, the determinant and the trace of $J(x^*, y^*)$ must both be positive.
Therefore observe that:

$$\Delta = \phi(x^*)g'(x^*)\eta(y^*)\psi'(y^*) + \eta(y^*)q'(x^*)\phi(x^*)\xi'(y^*)$$

which is positive if

$$\phi(x^*)\eta(y^*)(g'(x^*)\psi'(y^*) + q'(x^*)\xi'(y^*)) > 0$$
$$g'(x^*)\psi'(y^*) + q'(x^*)\xi'(y^*) > 0$$

and

$$\tau = \phi(x^*)g'(x^*) + \eta(y^*)\psi'(y^*) > 0.$$

Furthermore if $g'(x^*) < 0$ then $\tau < 0$, since by assumption $\psi'(y^*) < 0$ so that $g'(x^*) > 0$. So that E^* will be unstable if Conditions (9) are met. In the following example the respective conditions for the existence, uniqueness and instability of the equilibrium in the population quadrant is stated, followed by a numerical and graphical representation of the results.

3.3 Huang, Wang and Zhu model

A special case of the Huang and Zhu model is suggested by Huang, Wang and Zhu [18].

$$\begin{aligned} \dot{x} &= x(a_1 + a_2 x - a_3 x^2) - sxy \\ \dot{y} &= y(-1 + x - y) \end{aligned} \tag{10}$$

in which it is assumed that $a_1 \geq 0$, $a_3 > 0$, $s > 0$ and the sign of a_2 is undetermined. This model supports a Holling type I functional response in the form of sx and a quadratic function $g(x)$ defined in such a way that it satisfies assumption (H1a). The function $g(x)$ is a quadratic function with one positive root $K = (a_2 + \sqrt{a_2^2 + 4a_1a_3})/2a_3$ and maximum value of $a_1 + a_2^2/4a_3$. System (10) has six equilibrium points namely: $E_0 = (0,0), E_1 = (x_1, 0), E_2 = (x_2, 0), E_3 = (x_3, x_3 - 1), E_4 = (x_4, x_4 - 1)$ and $E_5 = (0, -1)$ where:

$$x_{1,2} = \left(a_2 \mp \sqrt{a_2^2 + 4a_1a_3}\right)/2a_3$$
$$x_{3,4} = (a_2 - s) \mp \sqrt{(a_2 - s)^2 + 4(a_1 + s)a_3}/2a_3$$

It is easy to confirm that E_3 will always be a saddle point and can therefore not have bounded solutions. The only other equilibrium point that might lead to co-existence of both species is E_4. To ensure the existence of a unique equilibrium point in the population quadrant, both x_4 and $x_4 - 1$ must be positive. Let $x_4 > 1$, that is

$$\begin{aligned}(a_2-s)+\sqrt{(a_2-s)^2+4(a_1+s)a_3} &> 2a_3\\ s^2 - 2sa_2 + 4a_3s + a_2^2 + 4a_1a_3 &> s^2-2sa_2+4sa_3+a_2^2-4a_2a_3+4a_3^2\\ a_1 + a_2 &> a_3\end{aligned}$$

This then becomes an additional assumption along with $a_1 \geq 0$, $a_3 > 0$ and $s > 0$. Now the unique equilibrium point in the population quadrant is $E^*(x^*, y^*)$ with

$$x^* = ((a_2 - s) + \sqrt{\beta})/2a_3$$

and

$$y^* = x^* - 1$$

where

$$\beta = (a_2 - s)^2 + 4(a_1 + s)a_3.$$

To confirm the existence of an invariant region rewrite System (10) by identifying the components and comparing them to the Huang and Zhu model as set out in Section 3.1.

$$\begin{array}{ll} g(x) = a_1 + a_2x - a_3x^2 \Rightarrow g'(x) = a_2 - 2a_3x & \\ \phi(x) = x \Rightarrow \phi'(x) = 1 & q(x) = x \Rightarrow q'(x) = 1\\ \xi(y) = sy \Rightarrow \xi'(y) = s & \eta(y) = y \Rightarrow \eta'(y) = 1\\ \gamma = 1 & \psi(y) = -y \Rightarrow \psi'(y) = -1 \end{array}$$

The function $g(x)$ is a quadratic function with one positive root $K = a_2 + \sqrt{a_2^2 + 4a_1a_3}/2a_3$ and it is bounded with a maximum value $a_1 + a_2^2/4a_3$. Therefore there exists a K so that $g(x) > 0$ on $[0, K)$, $g(K) = 0$ and $g(x) < 0$ on (K, ∞) and as before $x(t)$ is bounded by K. Since $\phi(x) = q(x) = x$ both ϕ and q are also bounded by K. All conditions (H1a) to (H1c) and (H1a) and (H1b) are met and as before an invariant region exists. Satisfying the Conditions (9) to ensure an unstable equilibrium the following must be upheld:

$$
\begin{aligned}
-(a_2 - 2a_3x^*) + s &> 0 \\
x^*(a_2 - 2a_3x^*) - y^* &> 0 \\
a_2 - 2a_3x^* &> 0
\end{aligned}
$$

Substituting x^* and y^* , into the conditions above we find that the equilibrium E^* will be an unstable equilibrium if:

$$\sqrt{\beta} > 0 \tag{11}$$

$$(a_2 - s + \sqrt{\beta})(s - \sqrt{\beta}) > a_2 - s + \sqrt{\beta} - 2a_3 \tag{12}$$

$$s - \sqrt{\beta} > 0 \tag{13}$$

are all satisfied.

Firstly observe that $\beta = (a_2 - s)^2 + 4(a_1 + s)a_3 > 0$ for all $a_1 \geq 0, a_3 > 0, s > 0$ and for any value a_2. So that $\sqrt{\beta}$ exists and is positive. Thus Condition (11) is satisfied.

Condition (12) will be satisfied if:

$$
\begin{aligned}
sa_2 - \beta + 2s\sqrt{\beta} - \sqrt{\beta}a_2 - s^2 - (a_2 - s + \sqrt{\beta} - 2a_3) &> 0 \\
-\beta + (2s - a_2 - 1)\sqrt{\beta} + (s - a_2 + 2a_3 + sa_2 - s^2) &> 0 \\
-(a_2 - s)^2 - 4(a_1 + s)a_3 + (2s - a_2 - 1)\sqrt{\beta} + s - a_2 + 2a_3 + sa_2 - s^2 &> 0 \\
\frac{-s^2 + 2sa_2 - a_2^2}{2a_3} - \frac{4(a_1 + s)a_3}{2a_3} + \frac{(2s - a_2 - 1)\sqrt{\beta}}{2a_3} + \frac{s - a_2 + sa_2 - s^2}{2a_3} + 1 &> 0 \\
\frac{-s^2 + 3sa_2 - a_2^2 + s - a_2}{2a_3} - 2(a_1 + s) + \frac{(2s - a_2 - 1)\sqrt{\beta}}{2a_3} + 1 &> 0 \\
\frac{(a_2 - s)(2s - a_2 - 1)}{2a_3} + \frac{(2s - a_2 - 1)\sqrt{\beta}}{2a_3} + 1 - 2a_1 - 2s &> 0 \\
(2s - a_2 - 1)\frac{(a_2 - s) + \sqrt{\beta}}{2a_3} + (1 - 2a_1 - 2s) &> 0 \\
(2s - a_2 - 1)x^* + (1 - 2a_1 - 2s) &> 0
\end{aligned}
$$

This is the same result achieved by Huang, Wang and Zhu by transforming System (10) into a system of Liénard equations [18]. For Condition (13) consider

$$s - \sqrt{\beta} > 0 \Rightarrow s^2 > \beta \Rightarrow s(2a_2 - 4a_3) > a_2^2 + 4a_1a_3$$

and assuming that $a_3 < a_2/2$ then

$$s > \frac{a_2^2 + 4a_1a_3}{2a_2 - 4a_3}.$$

The main result of Huang, Wang and Zhu states that: "When $a_1+a_2 > a_3$ and $s > 1$, the necessary and sufficient condition, if there exists one and only one limit cycle, is $(2s - a_2 - 1)x^* + (1 - 2a_1 - 2s) > 0$." We can now extend on that theorem as follows:

Given that $a_1 \geq 0, a_3 > 0, s > 0$ and $a_1 + a_2 > a_3$, System (10) will possess at least one limit cycle if

$$(2s - a_2 - 1)x^* + (1 - 2a_1 - 2s) > 0 \tag{14}$$

and

$$s > \frac{a_2^2 + 4a_1a_3}{2a_2 - 4a_3}. \tag{15}$$

To illustrate graphically, choose parameters for each of the variables so that the equations in (14) and (15) are satisfied. The choice is not a true reflection of any ecological data but rather for demonstrative purposes.
Let $a_1 = 10; a_2 = 7; a_3 = 2$ and $s = 32$. Then the carrying capacity of the prey is $K = 5.34$, the equilibrium point $E^* = (1.5, 0.5)$ and a limit cycle is evident as shown in Figure 7.

4 Conclusion

Recently many disciplines lean towards predator-prey models when cyclic behaviour in their fields of research is observed. However,

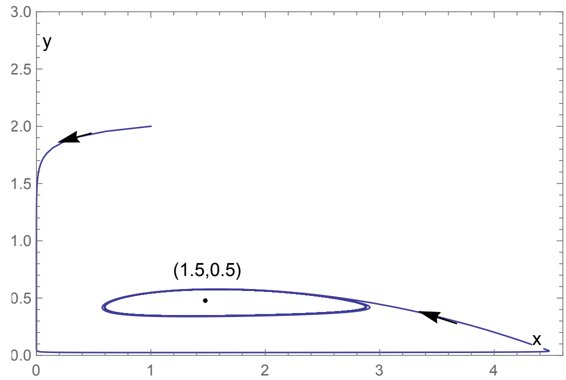

Figure 7: Limit cycle for the Huang, Wang and Zhu model with initial value $(1, 2)$ and $E^* = (1.5, 0.5)$.

the study of differential equations covered in elementary mathematics courses does not equip students in the fields of biology, ecology or economics to investigate stability or possible existence of limit cycles in their models. Traditional methods usually employed include choosing suitable Dulac functions where a certain degree of luck or clever insight is needed. Performing transformations to systems of generalized Liénard equations, where results concerning boundedness are well known, is certainly not always accessible to the less experienced who may not be familiar with these techniques. Furthermore, if Poincaré-Bendixson theory is to be applied, the challenge is to show that an invariant region exists. Zill and Cullen [9] state the following categorically: "The problem of finding an invariant region for a nonlinear system is an extremely difficult one." However, once the existence of an invariant region has been established, the investigation of stability or the existence of limit cycles reduces to basic eigenvalue analysis. The ELC addresses these problems by simply identifying the properties of the functions comprising the predator-prey system of differential equations in order to prove or disprove the existence of an invariant region. The technique determines the boundedness of solutions almost at a glance and will therefore be accessible to scholars from disciplines other that mathematics.

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