AE454 Literature Review - Limit Cycles in Predator-Prey Communities

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B, b, c, f, K, k, r	=	parameters for original system
$\alpha, \beta, \delta, \gamma$	=	parameters for nondimensionalized system
λ	=	eigenvalue of the system
x, y	=	state variables for original system
$\bar{x}, \bar{y}$	=	equilibrium state
x^*, y^*	=	state variables for nondimensionalized system

I. Introduction

Predator-prey systems are a very interesting type of dynamical system, one of which I was not aware of its complexity and predictability until the topic was brought up in class as an example. The fact that we can use methods often used to analyze mechanical systems to interpret these and that we predict population changes with it is a very interesting feat stemming from this crossing between biology and mathematics. In this paper, I aim to review Robert M. May's paper on the existence of "Limit Cycles in Predator-Prey Communities" [2], particularly focusing on discussing his argument about the stability of limit cycles found on unstable nonlinear differential equation systems. I will then continue the analysis of the same system mentioned in [2], making observations similar to the ones mentioned in Michael E. Gilpin's "Enriched Predator-Prey Systems: Theoretical Stability " [1], focusing on the system's behavior near Hopf bifurcations. The sources I will discuss differ in the sense that [2] focuses on the existence of limit cycles, and the fact that those are asymptotically stable equilibrium trajectories when one of the eigenvalues for the predator-prey system turns unstable, whereas [1] focuses on the system's behavior on either side of a Hopf bifurcation. I aim to reproduce their results via simulation and make my own observations. These papers relate to topics discussed in class as we have discussed predator-prey systems before but with simpler dynamics than the ones presented in these papers. They also relate to the discussions of Hopf bifurcations that we did in the last few lectures, so exploring these papers will allow me to get a deeper understanding of this very interesting topic.

The system I will be discussing is as follows:

$$\frac{dx}{dt} = rx - \frac{r}{K}x^2 - ky - kye^{-cx} \tag{1}$$

$$\frac{dy}{dt} = -by + By - Bye^{-fx} \tag{2}$$

II. Topic Significance

The parameters in (1) and (2) describe system quantities such as predation rate, reproduction rate, and others. Those parameters affect the system in such a way that they can determine whether the populations will die out and converge to an equilibrium, or oscillate over time. These oscillations were often considered the behavior of an unstable system until it was shown that the oscillatory behavior describes stable limit cycles when plotted in phase space, and different initial states would converge to those limit cycles over time. Understanding this property is pivotal for a better understanding of the real system that these equations describe. This understanding allows scientists to better predict environmental fluctuations and the development of better conservation strategies for specific ecosystems. In an era of increasing environmental challenges, this knowledge is essential for informed decision-making and effective conservation practices.

III. Mathematical Analysis

Let's begin our analysis of the system described by (1) and (2). To start, we can easily see that the system has two equilibria, one at $(0,0)$ and another at $(K,0)$. For analysing their respective stabilities, we will linearize the system about those points by takign the Jacobian. We can see below that the eigenvalues for the linearization at $(0,0)$ are at $\lambda^{\pm} = r, -b$. Assuming all parameters in our system are positive, we should expect the origin to be unstable.

$$
\begin{aligned}
A &= \left.\begin{bmatrix} \frac{d\dot{x}}{dx} & \frac{d\dot{y}}{dx} \\ \frac{d\dot{x}}{dy} & \frac{d\dot{y}}{dy} \end{bmatrix}\right|_{(\bar{x},\bar{y})=(0,0)} \\
&= \begin{bmatrix} r & 0 \\ 0 & -b \end{bmatrix}
\end{aligned}
$$

Similarly, we can linearize the system about $(K,0)$. As can be seen below, certain choices of parameters could take the system from stability to instability.

$$
\begin{aligned}
A &= \begin{bmatrix} \frac{d\dot{x}}{dx} & \frac{d\dot{y}}{dx} \\ \frac{d\dot{x}}{dy} & \frac{d\dot{y}}{dy} \end{bmatrix}_{(\bar{x},\bar{y})=(K,0)} \\
&= \begin{bmatrix} -r & -k\left(1-e^{-cK}\right) \\ 0 & -b+B\left(1-e^{-fK}\right) \end{bmatrix}
\end{aligned}
$$

This system contains 7 parameters that can affect its behavior. These many parameters can make analysis complicated, as well as potentially require large computation costs. It is in our best interest to simplify the system by nondimensionalizing it, which would make the system simpler and make its analysis more generalized. I simplified the system down to 4 nondimensional variables, and this system can be seen below, with x^* and y^* being the nondimensionalized state variables.

$$
\frac{dx^*}{dt^*} = x^* - x^{*2} - y^*(1-e^{-\alpha x^*}) \tag{3}
$$

$$
\frac{dy^*}{dt^*} = -\delta y^* + \gamma y^*(1-e^{-\beta x^*}) \tag{4}
$$

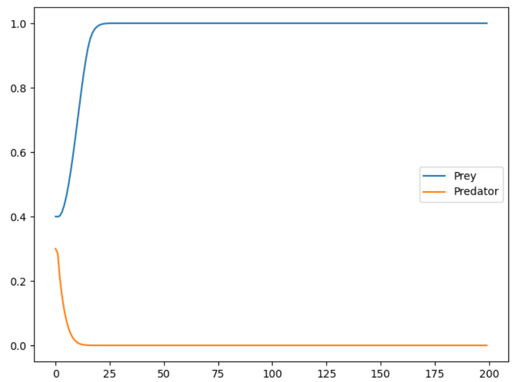
This system's new equilibria are at $(0,0)$ and $(1,0)$, with equal stability as that in the original system, as expected. We find the eigenvalue pairs to be $[1, -\delta]$ and $[-1, -\delta + \gamma(1-e^{-\beta})]$ respectively. The new linearized systems can be seen below:

$$
\begin{aligned}
A &= \begin{bmatrix} \frac{d\dot{x}^*}{dx^*} & \frac{d\dot{y}^*}{dx^*} \\ \frac{d\dot{x}^*}{dy^*} & \frac{d\dot{y}^*}{dy^*} \end{bmatrix}_{(\bar{x},\bar{y})=(0,0)} &= \begin{bmatrix} 1 & 0 \\ 0 & -\delta \end{bmatrix} \\
A &= \begin{bmatrix} \frac{d\dot{x}^*}{dx^*} & \frac{d\dot{y}^*}{dx^*} \\ \frac{d\dot{x}^*}{dy^*} & \frac{d\dot{y}^*}{dy^*} \end{bmatrix}_{(\bar{x},\bar{y})=(1,0)} &= \begin{bmatrix} -1 & e^{-\alpha}-1 \\ 0 & -\delta+\gamma\left(1-e^{-\beta}\right) \end{bmatrix}
\end{aligned}
$$

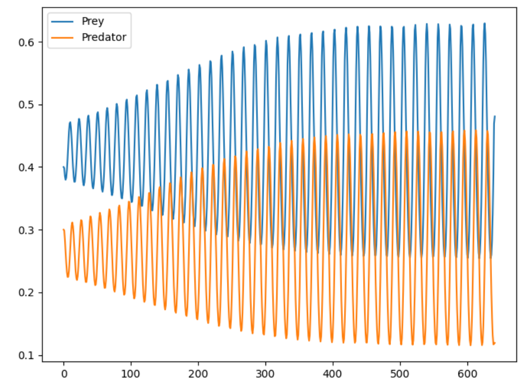
For the purposes of analyzing the effects of changing parameters on the behavior of the predator-prey system, we will keep

$$
\alpha = 2, \delta = 2, \gamma = 3.5
$$

fixed, and modify only β. By plugging those values into our eigenvalue calculations, we find that the equilibrium $(1,0)$ is stable if $\beta > \ln(7/3)$ (aka there is a Hopf bifurcation at $\beta = \ln(7/3)$), and it should form a limit cycle otherwise. Below we can see plots showing how the predator and prey populations change as a function of time for stable and "unstable" β.



(a) Plot showing how the system evolves for $\beta = 0$.



(b) Plot showing how the system evolves for $\beta = 2$.

Fig. 1 Plots showing stable and oscillating systems over time.

For Fig. 1a we see that the prey population approaches 1 over time, and the predators go extinct, thus reaching the predicted equilibrium of $(1, 0)$. Fig. 1b shows how the system behaves when one of the eigenvalues is positive, thus creating a limit cycle. We can see that over time the amplitudes of the oscillations seem to stabilize. Below, we can see what this looks like in phase space.

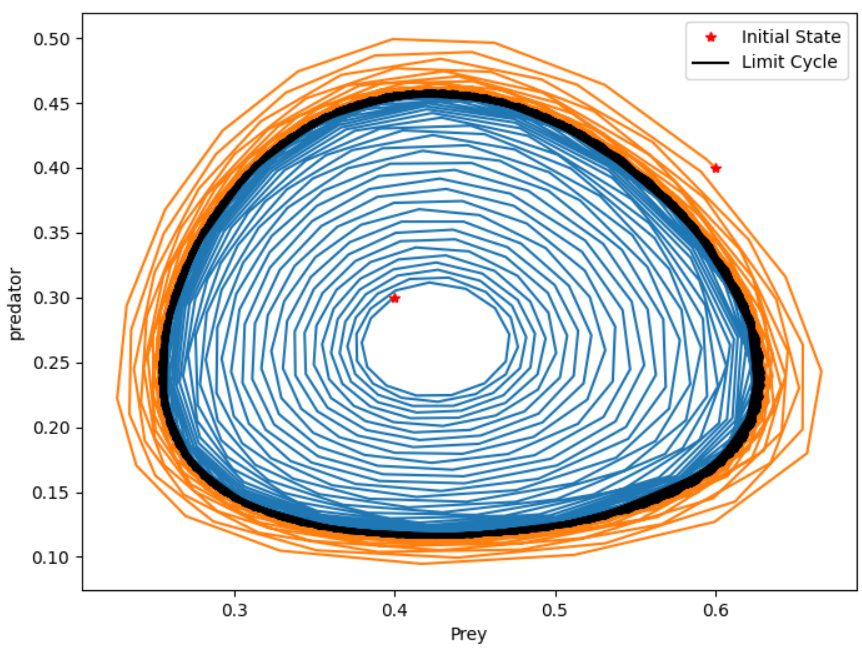


Fig. 2 Plot showing the limit cycle for $\beta = 2$, as well as two trajectories showing the convergence of the trajectories initialized inside and outside of the limit cycle. The red stars show the initial states of the trajectories, showing how the systems move counterclockwise.

Fig. 2 shows how the system does have a stable limit cycle. The red stars are placed at the initial state of the trajectories, confirming that the trajectories do converge to the limit cycle as time approaches infinity. We can note the asymptotic convergence by comparing the density of the blue and orange lines as they get more clustered as the trajectories approach the limit cycle.

Earlier, we calculated that a Hopf bifurcation should occur when $\beta = \ln(7/3)$. We then saw in Fig. 1 that the system is stable at $\beta = 0$ and oscillates at $\beta = 2$ as we expected. Below, we can see a plot showing how the system's dynamics change as we vary β near the Hopf bifurcation point.

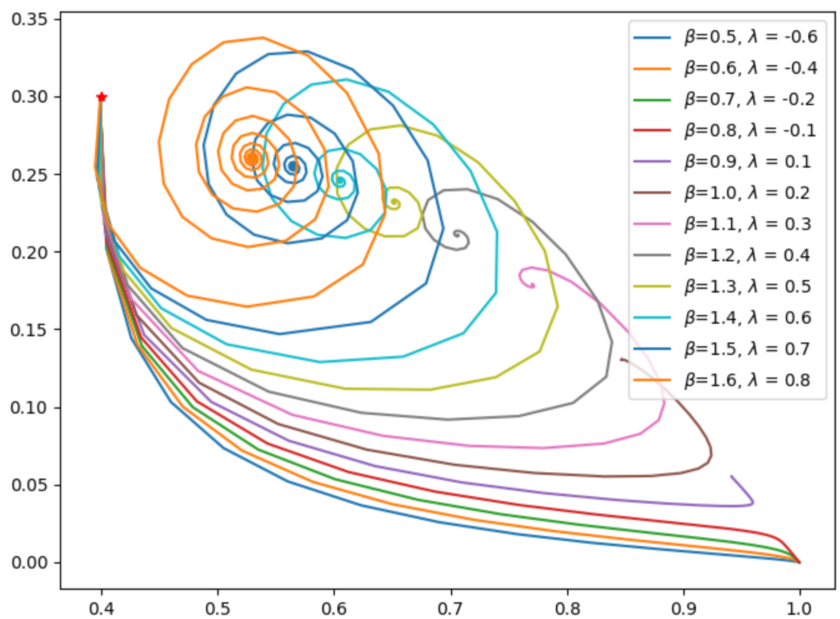


Fig. 3 System behavior for varying β from 0.5 to 1.6, with the initial state at $(0.4, 0.3)$.

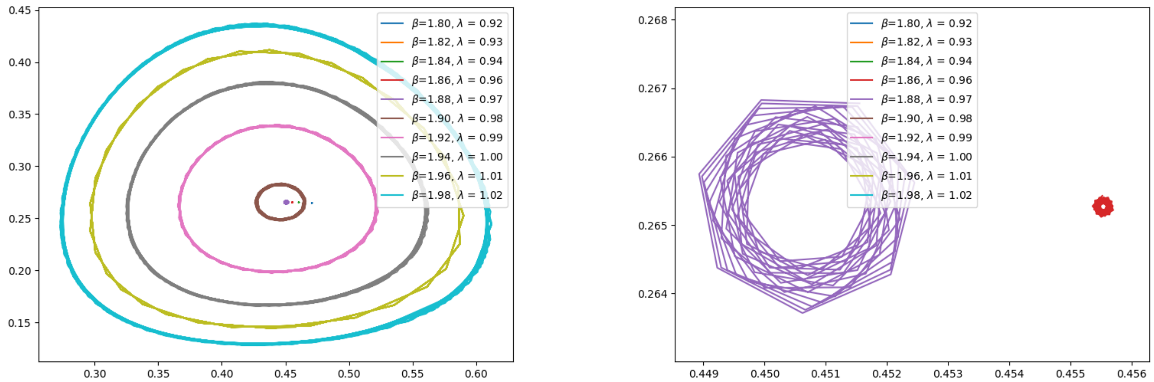
We can see that for all β values under the Hopf bifurcation value, the system is stable and tends to the extinction of the predator, ending at $(1, 0)$. As soon as β passes the threshold, the system's equilibrium begins shifting away from the stable equilibrium and spirals towards different equilibria. The new equilibria, or the point where the "unstable" system converges, happens exactly at the intersection of the system's isoclines, which are at

$$x^* = \frac{-\ln\left(1 - \frac{\delta}{\gamma}\right)}{\beta} \tag{5}$$

$$y^* = \frac{x^*(1 - x^*)}{1 - e^{-\alpha x^*}}. \tag{6}$$

When those spirals become limit cycles, the intersection of the isoclines will be at exactly the center of the cycle.

Below we can see how the system evolves for larger values of β.



(a) Plot showing the effect of β on the system's limit cycle, from $\beta = 1.80$ to $\beta = 1.98$.

(b) Plot showing the limit cycles for $\beta = 1.86, 1.88$.

Fig. 4 Plots showing the effect of changing β on the shape and size of the limit cycle.

It seems as though the system's limit cycle experiences the largest changes in size when the affected eigenvalue is near 1, perhaps due to being the additive inverse of the stable eigenvalue in the linearized system. In Fig. 4a we see the large limit cycles formed, with little dots to the right of the center of the larger cycles. Fig. 4b shows the zoomed-in limit cycles for $\beta = 1.86, 1.88$. As we can see, in the left image, although it seems like they are equilibrium points, we can see that they are actually just very small cycles.

IV. Conclusion

This paper has navigated the complex dynamics of predator-prey systems with a focus on the existence and stability of limit cycles by reviewing Robert M. May's seminal work on "Limit Cycles in Predator-Prey Communities" and drawing insights from Michael E. Gilpin's exploration of enriched predator-prey systems. Our analysis of the predator-prey system, as described by the differential equations (1) and (2), revealed the presence of equilibria at (0,0) and (K,0) and showcased their stability properties through linearization. Nondimensionalization proved to be a pivotal step, simplifying the system, reducing parameters, and allowing for a more generalized understanding of the predator-prey system's dynamics.

Simulation results not only validated theoretical predictions but also demonstrated the practical implications of limit cycles and Hopf bifurcations. The stability of limit cycles and the system's behavior near bifurcation points carry deep ecological significance, influencing the long-term coexistence of predator and prey populations. Our exploration of varying parameters, particularly focusing on the effects of changing β near the Hopf bifurcation point, provided valuable insights into the differences between stable equilibria and limit cycles. The plots illustrate the transitions, highlighting the system's behavior as it converges to equilibria or spirals into stable limit cycles. This discussion on predator-prey systems contributes not only to theoretical ecology but also to the practical realm of conservation.

Understanding the stability and oscillatory behaviors in these systems gives scientists and policymakers tools for predicting environmental fluctuations and developing informed conservation strategies. As our planet faces growing environmental challenges, the knowledge gained from this analysis becomes essential for effective decision-making and sustainable ecological management. Essentially, the exploration of limit cycles in predator-prey systems serves as a bridge between theoretical abstraction and real-world application. The behavior of these populations, captured in mathematical models and validated through simulations, furthers our comprehension of ecological dynamics.

Acknowledgments

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References

[1] Michael E. Gilpin. “Enriched Predator-Prey Systems: Theoretical Stability”. In: *Science* 177.4052 (1972), pp. 902–904. DOI: 10.1126/science.177.4052.902. eprint: https://www.science.org/doi/pdf/10.1126/science.177.4052.902. URL: https://www.science.org/doi/abs/10.1126/science.177.4052.902.

[2] Robert M. May. “Limit Cycles in Predator-Prey Communities”. In: *Science* 177.4052 (1972), pp. 900–902. DOI: 10.1126/science.177.4052.900. eprint: https://www.science.org/doi/pdf/10.1126/science.177.4052.900. URL: https://www.science.org/doi/abs/10.1126/science.177.4052.900.