Impact of Delay on Predator-Prey Models

A. Moujahid\textsuperscript{1}, F. Vadillo\textsuperscript{1,}\textsuperscript{*}

Department of Mathematics, University of the Basque Country

Abstract

Mathematical modeling based on time-delay differential equations is an important tool to study the role of delay in biological systems and to evaluate its impact on the asymptotic behavior of their dynamics. Delays are indeed found in many biological, physical, and engineering systems and are a consequence of the limited speed at which physiological, chemical, or biological processes are transmitted from one place to another. Since real biological systems are always subject to perturbations that are not fully understood or cannot be explicitly modeled, stochastic delay differential systems (SDDEs) provide a more realistic approximation to these models. In this work, we study the predator-prey system considering three time delay models: one deterministic and two types of stochastic models. Our numerical results show relevant differences in their respective asymptotic behaviors.

Keywords: Epidemic Dynamics, Delay Differential Equations, Stochastic Delay Differential Equations.

2010 MSC: 92D30, 34K99, 34F99, 60H30

1. Introduction

In recent years, life sciences have been the focus of numerous research activities to achieve a better understanding of many phenomena of life and the interaction between living systems and the environment. In this context, mathematical modeling based on differential equations, especially stochastic differential equations with time delay, is an important tool for the study of biological and ecological systems. Mathematical models in population dynamics is a topic that began many years ago, and there is an extensive bibliography. Two classic references include. \cite{14, Chap. 1} from 1973 and also \cite{16, Chap. 1} from 1989, this topic even appears in introductory courses on differential equations, (see, e.g., \cite{23, pp. 284} or \cite{3, pp. 74}). Four textbooks of interest are \cite{8}.

\textsuperscript{*}Corresponding authors

Email addresses: abdelmalik.moujahid@ehu.eus (A. Moujahid), fernando.vadillo@ehu.eus (F. Vadillo)

Preprint submitted to Elsevier March 25, 2022
[17], [22], and [5], which help students explore and discover mathematical concepts and apply these concepts in building and analyzing mathematical models in life science disciplines such as biology, ecology, and environmental science.

However, many of these models ignore some hidden processes and external influences that are poorly understood and generally affect the dynamics of these systems. Therefore, for a more realistic interpretation and approximation to real systems, it is necessary to consider stochastic delay differential equations [2, 1, 4, 18] and [20], where the relevant mechanisms are modeled as stochastic processes.

On the other hand, delayed interacting processes are ubiquitous in many biological systems, which generally consist of interacting units, and depending on the time scales of these units, the speed of information propagation becomes relevant to their dynamics. Therefore, delayed stochastic differential equations are crucial for the study and better understanding of these systems. Moreover, it is almost self-evident that the introduction of memory terms greatly increases the complexity.

The rest of the paper is organized as follows. In Section 2, we present the deterministic model for the prey-predator system and study its asymptotic behavior as a function of time delay. Section 3 describes the first delayed stochastic model constructed by adding Gaussian noise to the deterministic terms. The second delayed stochastic model, based on probabilistic considerations, is derived in Section 4. We conclude in Section 5 and draw the main contributions as well as possible future applications to more complex systems with more parameters.

2. The Prey-Predator Deterministic Model

The predator-prey model was originally proposed by A. J. Lotka and V. Volterra in the 1920s. Since then, many other models have been proposed with different functional responses. In this paper, we consider the Michaelis-Menten type predator-prey model introduced by Freedman [9] in 1980. The time-delay dynamics of this model is governed by the following system of differential equations,

$$\begin{align*}
\frac{dx}{dt} &= r x(t) \left(1 - \frac{x(t)}{K}\right) - \frac{\beta x(t) y(t - \tau)}{1 + \sigma x(t)}, \\
\frac{dy}{dt} &= \frac{\beta x(t) y(t - \tau)}{1 + \sigma x(t)} - a y(t),
\end{align*}$$

where $x(t)$ and $y(t)$ represent the population densities of the prey and predator, respectively. The prey population is assumed to have logistic growth with a carrying capacity $K$ and a specific growth rate constant $r$. The feeding rate $\beta$ is the maximum number of prey that can be eaten by a predator in any unit of time, $r$ is a specific growth rate, $\sigma$ is a positive constant describing the effects of capture rate, and $a$ refers to the dead rate for the predator.

The initial conditions are set to $x(0) > 0$ and $y(t) = \psi(t) > 0$ when $t \in [-\tau, 0]$, where $\psi(t)$ is a smooth function and $\tau$ the time delay. In [19, pp. 217] it is shown that there
are three fixed points: the trivial equilibrium \( \mathcal{E}_0 = (0, 0) \), the semi-trivial equilibrium \( \mathcal{E}_1 = (K, 0) \), and the interior equilibrium \( \mathcal{E}_+ = (x^*, y^*) \), with
\[
\begin{align*}
x^* &= \frac{a}{\beta - \sigma a}, & y^* &= \frac{r(x^*)^2}{K a} (R_0 - 1), \quad \text{and} \quad R_0 = \frac{K}{x^*}.
\end{align*}
\]
The stability theorem \([19, \text{Th. 11.2}]\) of this interior equilibrium shows that \( \mathcal{E}_+ = (x^*, y^*) \) is locally stable when \( 1 < R_0 \leq R_c = 2 + \frac{1}{1 + 2\sigma x^*} \), while for \( 1 < R_c < R_0 \), there exist a bifurcation \( \tau^* > 0 \) such that the equilibrium is asymptotically stable for values of \( \tau \in [0, \tau^*] \), and unstable when \( \tau > \tau^* \).

Figure 1 shows the phase portraits of the deterministic system given by Eq. (1) for different values of the time-delay \( \tau \) and for the parameter values \( r = 0.8, \ K = 5, \ \sigma = 0.01, \ \beta = 0.5, \ a = 0.3 \) \([21]\). For these values, the interior equilibrium is \( (x^*, y^*) = (0.6036, 1.4153) \), \( R_0 = 8.2833 \) and \( R_c = 2.9881 \). This corresponds to the case where \( 1 < R_c < R_0 \). As can be seen, there is a critical value of \( \tau \), the system switches from a stable fixed point to a limit cycle.

To better visualize these bifurcation patterns, we also plotted the bifurcation diagram with \( \tau \) as a varying parameter (see Figure 2). According to our numerical results, the interior equilibrium is asymptotically stable for values of \( \tau \) smaller than the bifurcation value \( \tau^* = 0.46 \) at which the Hopf bifurcation occurs. At this critical value, the trajectories of the system slowly converge toward the limit cycle, while for values of \( \tau \) larger than \( \tau^* \), the behavior of the system quickly collapses into the limit cycle (see Figure 1).

3. White noise based stochastic model: Model 1

From a biological perspective, the inclusion of stochastic perturbations in the deterministic predator-prey model \([11]\) allows for a more realistic interpretation of the system. The simplest way to do this is to add a white noise that is proportional to \( x(t) \) and \( y(t) \), leading to the SDDE:
\[
\begin{align*}
\frac{dx(t)}{dt} &= \left[ r x(t) \left( 1 - \frac{x(t)}{K} \right) - \frac{\beta x(t) y(t - \tau)}{1 + \sigma x(t)} \right] dt + v_1 x(t) \, dW_1(t), \\
\frac{dy(t)}{dt} &= \left[ \frac{\beta x(t) y(t - \tau)}{1 + \sigma x(t)} - a y(t) \right] dt + v_2 y(t) \, dW_2(t),
\end{align*}
\]
where \( W_1(t) \) and \( W_2(t) \) denote two independent Brownian motions, and the positive constants \( v_1 \) and \( v_2 \) refer to the intensities of the white noises.

The numerical simulations use Milstein’s scheme for SDDEs, discussed in \([12]\) or \([13, \text{p. 137}]\), actually it is a simple adaptation of the method for SDE of the same name which can be found in classical texts, e.g. \([10]\), \([13]\), and more recently \([11]\).

In Figure 3 we plotted the phase portraits the model for different values of the time delay \( \tau \). The results were obtained from the stochastic data over 500 simulations and \( 0 \leq t \leq 1500 \). As you can see (panel (ii)), for each value of \( \tau \), the trajectories approach different fixed points, and no Hopf bifurcation is observed. In other words,
Figure 1: Phase portraits of the model at different time-delays. \( \tau = 0.8, K = 5, \sigma = 0.01, \beta = 0.5, a = 0.3 \Rightarrow \tau^* = 0.46 \) and \( 0 \leq \tau \leq 10000 \). \( x(0) = 3, y(0) = 1 \)

Figure 2: Hopf bifurcation diagram of the deterministic system considering the time delay as a bifurcation parameter. For \( \tau < 0.46 \), the interior equilibrium is asymptotically stable. For \( \tau \geq 0.46 \) an asymptotically limit cycle emerges.

The time delay move the system to different regions of the state space where a particular stationary fixed point occurs.

To better understand how the time delay affects the system dynamics, we also plotted the long-term average evolution of the steady-state equilibrium as a function of the
time delay (see Figure 3). For each value of \( \tau \), the trajectories were averaged over 500 runs and \( 0 \leq t \leq 1500 \). For values of \( \tau \) less than \( \tau^{**} = 0.8 \), the prey population is on average smaller than the predator population, while for values greater than \( \tau^{**} \) the situation reverses and the predator population dominates the prey population. This value of \( \tau^{**} \) is of course dependent on the capture rate \( \sigma \), and increases with decreasing \( \sigma \). At the critical value \( \tau^{**} \), the population sizes of prey and predators are equal on average (see Figure 5).

4. Probabilistic stochastic model: Model 2

The second stochastic model that we will consider, which we could call the probabilistic model, is very similar to the ones analyzed in [7], [24], [6] and [15]. Assuming
Figure 5: Model 1: Long-term trajectories of the model for different values of the time delay $\tau$ for $\nu_1 = \nu_2 = 0.1$, $\nu_1 = \nu_2 = 0.1$, $r = 0.8$, $K = 5$, $\sigma = 1/3$, $\beta = 0.5$ and $a = 0.3$. The results were obtained from the stochastic data over 500 simulations and $0 \leq t \leq 1500$.

that the changes and their probabilities are those given in Table 1.

| Change | Propability |
|--------|-------------|
| $\Delta Z^{(1)} = (1, 0)^T$ | $p_1 = r x(t) \left(1 - \frac{x(t)}{K}\right) \Delta t$ |
| $\Delta Z^{(2)} = (-1, 0)^T$ | $p_2 = \frac{\beta x(t) Y(t-\tau)}{1 + \sigma x(t)} \Delta t$ |
| $\Delta Z^{(3)} = (0, 1)^T$ | $p_3 = \frac{\beta x(t) Y(t-\tau)}{1 + \sigma x(t)} \Delta t$ |
| $\Delta Z^{(4)} = (0, -1)^T$ | $p_4 = ay(t) \Delta t$ |

Table 1: Possible change in $Z = (X, Y)^T$ and their probabilities
Fixing $Z(t)$ at time $t$, we calculate the expected change for $Z = (X, Y)^T$ 

$$E(\Delta Z) = \sum_{j=1}^{4} p_j \Delta Z^{(j)} = \begin{pmatrix} r x(t) \left(1 - \frac{x(t)}{K}\right) - \beta x(t) y(t - \tau), & \frac{\beta x(t) y(t - \tau)}{1 + \sigma x(t)} - ay(t), \\ \frac{\beta x(t) y(t - \tau)}{1 + \sigma x(t)} - ay(t), & \end{pmatrix} \Delta t, \quad (3)$$

and the covariance matrix

$$E(\Delta Z(\Delta Z)^T) = \sum_{j=1}^{4} p_j (\Delta Z^{(j)}(\Delta Z^{(j)})^T) = D(x, y) \Delta t, \quad (4)$$

where $D(x, y)$ is the diffusion matrix

$$D = \begin{pmatrix} r x(t) \left(1 - \frac{x(t)}{K}\right) + \beta x(t) y(t - \tau) & 0 \\ 0 & \frac{\beta x(t) y(t - \tau)}{1 + \sigma x(t)} + ay(t) \end{pmatrix},$$

so we arrived at stochastic differential system

$$\begin{align*}
    dx(t) &= \left[ r x(t) \left(1 - \frac{x(t)}{K}\right) - \beta x(t) y(t - \tau) \right] dt + \sqrt{r x(t) \left(1 - \frac{x(t)}{K}\right) + \frac{\beta x(t) y(t - \tau)}{1 + \sigma x(t)}} \, dW_1(t), \\
    dy(t) &= \left[ \frac{\beta x(t) y(t - \tau)}{1 + \sigma x(t)} - ay(t) \right] dt + \sqrt{\frac{\beta x(t) y(t - \tau)}{1 + \sigma x(t)} + ay(t)} \, dW_2(t)
\end{align*} \quad (5)$$

In Figure 6, we have plotted the phase portraits of Model 2 for different values of $\tau$, ranging from low to higher values. The results correspond to an average of 100 trials with initial value $x(0) = 3, y(0) = 1$ and $0 \leq t \leq 9$. In this case, the predator population goes to extinction very quickly, and the time to extinction appears to increase with delay, showing a minimum for low values of $\tau$ (see Figure 7).

5. Conclusion

We have analysed the behaviour of two time-delayed stochastic differential systems for the prey-predator model and compared them with the corresponding deterministic system. The introduction of stochastic perturbations into these time-delayed models has a significant impact on population extinction and enriches the dynamics of the models. We found a significant difference between the deterministic system and the two classes of stochastic systems. Considering the time delay as a bifurcation parameter, the deterministic system exhibits a Hopf bifurcation leading to a critical $\tau^*$ from which the system transitions from the stable asymptotic fixed point to a stable limit cycle.

When the stochastic perturbation is modelled by simply adding a white noise to the deterministic components of the system (Model 1), the time delay appears to drive the system into different regions of state space where a particular stationary fixed point occurs, but no Hopf bifurcation is observed. Nevertheless, the population appears to
be persistent for both the deterministic system and the stochastic model 1. However, in contrast to what we observed previously, for the second stochastic system (Model 2) derived from a probabilistic approach, the system collapses rapidly and the population goes to extinction. This is consistent with previous work supporting the fact that the nature of the stochastic system has a significant impact on the asymptotic behavior of
the population, and environmental noise can cause the solution of the stochastic system to be extinct [24].

Acknowledgments
This work was supported by Spanish Ministry of Sciences Innovation and Universities with the project PGC2018-094522-B-100 and by the Basque Government with the project IT1247-19.

References
[1] E. Allen, *Modeling with Itô Stochastic Differential Equations*, Springer, 2007.
[2] L.J.S. Allen, *An Introduction to Stochastic Processes with Applications to Biology*, Person Prentice Hall, 2003.
[3] W. Boyce and R. Diprima, *Elementary Differential Equations and Boundary Value Problems*, 4rd ed., John Wiley and Sons, 1986.
[4] J.R. Chasnov, *Mathematical biology*, The Hong Kong University of Science and Technology, 2009.
[5] C.S. Chou and A. Friedman, *Introduction to Mathematical Biology: Modeling, Analysis, and Simulations*, Springer, 2016.
[6] F. de la Hoz, A. Doubova, and F. Vadillo, *Persistence-time Estimation for some Stochastic SIS Epidemic Models*, Discrete and Continuous Dynamical Systems Series B 20 (2015), no. 8, 2933–2947.
[7] F. de la Hoz and F. Vadillo, *A mean extinction-time estimate for a stochastic Lotka-Volterra predator-prey model*, Applied Mathematics and Computation 219 (2012), no. 1, 170–179.
[8] G. de Vries, T. Hillen, M. Lewis, J. Müller, and B. Schönfisch, *A Course in Mathematical Biology*, SIAM, 2006.
[9] H.I.Freedman, *Deterministic mathematical models in population ecology*, Canadian Journal of Statistics 10 (1982), no. 4, 315–315.
[10] D.J. Higham, *An Algorithmic Introduction to Numerical Simulation of Stochastic Differential Equations*, SIAM Review 43 (2001), no. 3, 525–546.
[11] D.J. Higham and E.K. Kloeden, *An Introduction to the Numerical Simulation of Stochastic Differential Equations*, SIAM, 2021.
[12] N. Hofmann and T. Müller-Gronbach, *A modified Milstein scheme for approximation of stochastic delay differential equations with constant time lag*, Journal of Computational and Applied Mathematics (2006), no. 197, 89–121.
[13] P.E. Kloeden and E. Platen, Numerical Solution of Stochastic Differential Equations, Cambridge University Press, 1998.

[14] R.M. May, Stability and Complexity in Model Ecosystems, Cambridge University Press, 1973.

[15] A. Moujahid and F. Vadillo, Modeling and Calibration for Stochastic Differential Models, Submitted (2021).

[16] J.D. Murray, Mathematical Biology I: An Introduction, 3rd ed., Springer-Verlag, 2002.

[17] D. Neal, Introduction to Population Biology, Cambridge University Press, 2004.

[18] E. Pardoux, Probabilistic Models of Population Evolution Scaling Limits, Genealogies and Interactions, Springer, 2016.

[19] F.A. Rihan, Delay Differential Equations and Applications to Biology, Springer, 2021.

[20] F.A. Rihan and H.J. Alsakaji, Stochastic Delay Differential Equations of Three-species System with Cooperation Among Prey Species, Discrete and Continuous Dynamics Systems Series S (2022), no. 15, 245–269.

[21] L.F. Shampine, I. Gladwell, and S. Thompson, Solving ODEs with MATLAB, Cambridge University Press, 2003.

[22] M. Sharin, Exploration of Mathematical Models in Biology with MATLAB, Wiley, 2014.

[23] G.F. Simmons, Differential Equations with Applications and Historical Notes, McGraw-Hill International Editions, 1972.

[24] F. Vadillo, Comparing stochastic Lotka-Volterra predator-prey models, Applied Mathematics and Computation 360 (2019), 181–189.