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Introduction to Chemical Oscillations Using a Modified Lotka Model

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Abstract: In teaching chemical kinetics most textbooks use the Lotka–Volterra Model to introduce the concept of chemical oscillations. Unfortunately, the Lotka–Volterra Model yields neutrally stable limit cycles for any initial conditions, which is a nonphysical property not observed in chemical kinetics. A more physical, two-variable model with simple linear stability analysis is, therefore, desirable. Here, we consider a Modified Lotka–Volterra Model that shows multiple physical steady states and both damped and stable oscillations. We can also study a stable node bifurcation to a saddle point and a stable node bifurcation to a stable limit cycle. This dynamically richer model can be analyzed through a simple linear stability analysis and numerical integration of the system of ordinary differential equations. Both methods, in particular the analytical analysis, are accessible to undergraduate students.

Introduction

Nowadays, most modern physical chemistry textbooks [1, 2] discuss nonlinear chemical kinetics. Although it is common practice to use the Lotka–Volterra Model (LVM) [3, 4] to introduce the concept of chemical oscillations, it is still recognized that the LVM is not an entirely optimal example of oscillations. On the one hand, it lacks a bifurcation relation, its oscillations only show marginal stability, and the LVM has a fixed point at infinity, which is nonphysical. On the other hand, a linear stability analysis is accessible to most undergraduates, making a simple two-variable model with stable oscillations and with a relatively simple stability analysis desirable.

In a past issue of this journal [5], we introduced the Higgins Model (HM) [6] as an alternative to the LVM. The HM is a more physical two-variable model in enzyme kinetics and a better example of chemical oscillations. In spite of the HM's physical foundation, its linear stability analysis is quite challenging and time-consuming for most undergraduates. To alleviate the cumbersome algebra associated with the HM, we introduce a Modified Lotka–Volterra Model (MLVM) as an alternative model to study chemical oscillations at the undergraduate level.

Even though a given Lotka–Volterra-type model has no chemical system associated with it, its linear stability analysis is simple compared to the analyses of any of the two-variable chemical models available. In addition, these types of models allow us to introduce several essential concepts in nonlinear chemical kinetics. First, we typically discuss the LVM in the classroom to introduce linear stability analysis. Second, we assign the analytical study of the MLVM as a problem set. This model shows multiple physical steady-state solutions, stable oscillations, and a simple bifurcation relation. In addition, all the linear stability analysis associated with this model is extremely accessible to undergraduates. Third, we study the MLVM numerically in a laboratory session. The numerical analysis can be carried out using any available software package capable of numerically integrating a system of differential equations. Finally, a laboratory report is required that should include several examples of the different bifurcations as well as the predictions derived from the analytical analysis. As a result, the students have a better sense of how the analytical and numerical analyses carried out in chemical kinetics complement each other. With this knowledge, the students are ready to study complex but more chemical models where, in many cases, only numerical integration is possible.

Although changes to the LVM are not new, none of the previous modified versions of the LVM [7] has been used to introduce chemical oscillations at the undergraduate level. Of the several modified models, we consider in Section II the changes to the LVM first suggested by Holling [8], which define the MLVM studied in this paper. In Section III, we use linear stability analysis to obtain a bifurcation relation among other results. This analysis yields dynamic information that is studied numerically in Section IV. We conclude with a discussion in Section V.

Modified Lotka–Volterra Model

Originally, Lotka introduced his model in 1920 [3] in relation to mass-action laws and chemical reactions. Six years later, Volterra used the same system of ordinary differential equations (ODEs) to study population dynamics. The model considers the interaction of only two species, the prey, G, and the predator, R. Considering G and R as the only measurable variables, the Lotka–Volterra Model is defined by the following ODEs:

$$\frac{dG}{dt} = k_o G - k_r GR \tag{1}$$

$$\frac{dR}{dt} = k_r GR - k_{rd} R \tag{2}$$

Equations 1 and 2 represent the LVM where k_o, k_r, and k_{rd} are rate constants. While the model became quite popular because of its simple mechanistic interpretation and simple linear analysis, it cannot truly show some of the most important concepts in nonlinear chemical dynamics. Notice that eqs 1 and 2 have a fixed point at infinity when R approaches the zero value, which means a prey exponential growth without a limit. In addition, as the prey population grows, the predator growth rate has no bounds.

In addition to these problems, a linear stability analysis, which is easy to do, yields marginal stable limit cycles. A limit cycle is the representation of the population oscillations in time when, instead of plotting G or R versus time, we plot prey versus predator populations. Moreover, if one applies a small change to G or R on a marginally stable limit cycle, the cycle will just shift to another limit cycle. Therefore, no initial condition will spiral in or out towards a limit cycle, which is a behavior observed in all chemical limit cycles. In spite of the simplicity of the LVM, a model with multiple physical steady states and stable limit cycles is desirable to introduce some of the most important concepts in nonlinear chemical kinetics at the undergraduate level.

Considering the simple physical interpretation of the Lotka–Volterra mechanism using the language of population dynamics, we discuss here a generalized Lotka–Volterra-type mechanism.

The model can be considered a modified LVM, but its modifications will yield more physical dynamic behaviors better suited to chemical kinetics. As in the classical LVM, we first consider the reproduction of the prey, G,

$$G \xrightarrow{k_g(G)} G + G \tag{3a}$$

where, in the general case, the rate of reproduction is a nonlinear function of the prey population. In the LVM, we simplify this functionality to a linear relation, that is, $k_g(G) = k_o(G)$. Second, we consider the predator, R, reproduction at the expense of the prey,

$$G + R \xrightarrow{k_r(G)} R + R \tag{3b}$$

Here, the rate is a nonlinear function of the prey and predator populations. Again, in the LVM, this rate is simplified to a quadratic relation linear in each of the prey and predator population, that is, k_rGR. Finally, we consider a simple predators death rate proportional to the predator population

$$R \xrightarrow{k_{rd}} \phi \tag{3c}$$

Eqs 3a–c constitute the Generalized Lotka–Volterra Model (GLVM). Different approximations can be made for the growth rates of the prey and predator, yielding several similar models [9].

Now we will consider specific changes that will remove some of the disadvantages of the Lotka–Volterra Model. For example, the fixed point at infinity is nonphysical. To remedy this problem, we consider that the prey reproduction follows a logistic growth. This growth translates into a prey-dependent rate constant,

$$k_g(G) = k_o(G_0 - G) \tag{4}$$

where G_o is the carrying capacity of the environment. The second modification considers expressions that includes an exponential predator growth in the abundance prey limit, that is, $G \gg 0$. This limiting exponential growth is attained using different expressions for the prey-dependent rate constant $k_r(G)$. In particular, we use the following expression first suggested by Hollings [8]:

$$k_r(G) = \frac{k_r}{K_g + G} \tag{5}$$

where $k_r(G)$ approaches zero as kr/G when $G \gg K_g$. Consequently, in this limit, eq 3b yields an exponential growth, k_rR. Using the previous changes given by eqs 4 and 5, we obtain the following ODEs associated with the Modified Lotka–Volterra Model:

$$\frac{dG}{dt} = k_o(G_o - G)G - \frac{k_rGR}{K_g + G} \equiv g_1(G,R) \tag{6}$$

$$\frac{dR}{dt} = \frac{k_rGR}{K_g + G} - k_{rd}R \equiv g_2(G,R) \tag{7}$$

Immediately we notice that the divergent fixed point in the LVM has been moved to (X_o, 0) in the MLVM. This point represents the extinction of the predator and the prey's maximum population; therefore, the three steady states of eqs 6 and 7, total extinction, predator extinction, and prey–predator coexistence, are more physical than the three steady states associated with the LVM. In addition, the prey's population is limited by the carrying capacity of the environment, G_o, and the predator growth rate is limited by an exponential growth k_rR.

Linear Stability Analysis

In this section, we present a linear stability analysis [7, 10] of the Modified Lotka–Volterra Model. For this purpose we scale the differential equation such that the dimensionless differential equations depend only on three parameters rather than five. Namely, we get from eqs 6 and 7:

$$\frac{dX}{d\tau} = r_o(X_o - X)X - \frac{kXY}{1+X} \equiv f_1(X,Y) \tag{8a}$$

$$\frac{dY}{d\tau} = \frac{kXY}{1+X} - Y \equiv f_2(X,Y) \tag{8b}$$

where we have defined the following dimensionless quantities:

$$\tau = \frac{t}{k_{rd}} \tag{9a}$$

$$X = \frac{G}{K_g} \tag{9b}$$

$$Y = \frac{R}{K_g} \tag{9c}$$

$$r_o = \frac{k_o K_g}{k_{rd}} \tag{9d}$$

$$k = \frac{k_r}{k_{rd}} \tag{9e}$$

In the first step of the stability analysis we find the steady-state solutions. In general, this is done by setting the left-hand side of the differential equations equal to zero, that is,

$$f_1(X^{ss}, Y^{ss}) = 0 \tag{10a}$$

$$f_2(X^{ss}, Y^{ss}) = 0 \tag{10b}$$

and solving for X^{ss} and Y^{ss}. From eqs 8a and 8b, we obtain three steady-state solutions. First, the trivial solution where both the prey and the predator are not able to survive,

$$X_1^{ss} = 0 \tag{11a}$$

$$Y_1^{ss} = 0 \tag{11b}$$

Second, the case when the predator is unable to survive,

$$X_2^{ss} = X_o \tag{12a}$$

$$Y_2^{ss} = 0 \tag{12b}$$

Finally, the prey–predator coexistence is given by:

$$X_3^{ss} = \frac{1}{k-1} \tag{13a}$$

$$Y_3^{ss} = r_o \frac{X_o(k-1)-1}{k-1} \tag{13b}$$

Clearly from eqs 13a and b, we can see that not only k has to be greater than one, but $X_o(k-1) > 1$ to get meaningful solutions; that is, X^{ss} and Y^{ss} have to be positive. From eq 9e, this condition means that the reproduction rate constant, k_r, has to be greater than the death rate constant, k_{rd}.

Once these stationary state solutions are obtained, stability analysis studies what happens to the dynamic variables X and Y when a steady-state solution is slightly perturbed. Namely, we want to know if the perturbations grow or die out. This knowledge is obtained by first calculating the relaxation matrix, R, which is the Jacobian associated with a set of ODEs [8]. This matrix is defined by the following equation:

$$R = \begin{pmatrix} \left(\frac{\partial f_1}{\partial X}\right)(X^{ss}, Y^{ss}) & \left(\frac{\partial f_1}{\partial Y}\right)(X^{ss}, Y^{ss}) \\ \left(\frac{\partial f_2}{\partial X}\right)(X^{ss}, Y^{ss}) & \left(\frac{\partial f_2}{\partial Y}\right)(X^{ss}, Y^{ss}) \end{pmatrix} \tag{14}$$

For the scaled MLVM, we obtained a simple relaxation matrix,

$$R = \begin{pmatrix} r_o(X_o - 2X^{ss}) - \frac{kY^{ss}}{(1+X^{ss})^2} & -\frac{kX^{ss}}{1+X^{ss}} \\ \frac{kY^{ss}}{(1+X^{ss})^2} & \frac{kX^{ss}}{1+X^{ss}} - 1 \end{pmatrix} \tag{15}$$

where X^{ss} and Y^{ss} are functions of the dimensionless parameters r_o, X_o, and k. In our case, we will end up with three matrices, one for each of the solutions of eqs 10a and 10b. Next, to find out the stability of each steady-state solution, we have to substitute the corresponding values of X^{ss} and Y^{ss} in eq 15. For example in the case of (X_3^{ss}, Y_3^{ss}), the relaxation matrix reduces to

$$R = \begin{pmatrix} \frac{r_o}{k}[X_o - \frac{k+1}{k-1} & -1 \\ \frac{r_o}{k}[X_o(k-1)-1] & 0 \end{pmatrix} \tag{16}$$

Finally, we have to find the corresponding eigenvalues for each of the three matrices. The analysis of the eigenvalues will yield the dynamic properties of each of the steady-state solutions. Finding the eigenvalues of R is equivalent to finding the solutions, λ, of the following equation.

$$|R - \lambda I| = 0 \tag{17}$$

where I is the identity matrix, and the vertical lines stand for the determinant. For any two variable models, eq 17 reduces to the following characteristic quadratic polynomial:

$$\lambda^2 - \mathrm{tr}R\lambda + \det R = 0 \tag{18}$$

where tr$R$ and det$R$ stand for the trace and determinant of R. Furthermore, the solutions of the quadratic equation are

$$\lambda_{\pm} = \tfrac{1}{2}\left(\mathrm{tr}R \pm \sqrt{(\mathrm{tr}R)^2 - 4\det R}\right) \tag{19}$$

From this equation we can infer general properties for any two-variable models. First, consider the case of a negative determinant, det$R < 0$. In this case we get two real eigenvalues, one positive and one negative. These two values imply that the steady-state solution is a saddle point. Second, we consider the case of a positive determinant of R and $4\det R < (\mathrm{tr}R)^2$. These two conditions imply two real eigenvalues, both either positive or negative. On one hand, if the trace is negative then both eigenvalues are negative, and we have a stable node. On the other hand, if the trace is positive then both eigenvalues are positive, and we have an unstable node. In the particular case when det$R = 0$, we obtain one zero eigenvalue and a second eigenvalue either negative or positive. These values define a saddle-node bifurcation point. Finally, we consider the case of a positive determinant and $4\det R > (\mathrm{tr}R)^2$. In this case, we have two imaginary eigenvalues, and the stability of the solutions is now determined by the real part, which in this case is given by

Table 1. Dimensionless Values

Parameter	Value
r_o	= 0.60
X_o	= 8.00
k	≈ 1.30

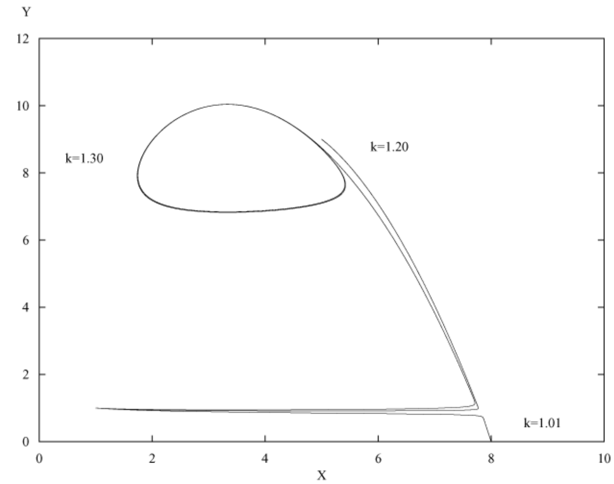

Figure 1. Phase-space representation of a transition through a bifurcation for the Modified Lotka–Volterra Model using parameters in Table 1 and different *k* values.

the trace of the relaxation matrix. Damped oscillations will be observed for a stable focus if the trace of R is negative. In contrast, the so-called spiraling out will be observed for an unstable focus if the trace of R is positive. In the latter case, the growing oscillations most likely will settle in a stable limit cycle.

Using eqs 11a and b in 15, we find a simple matrix that can be used in conjunction with eq 19 to find the following eigenvalues:

$$\lambda_-^1 = -1 \tag{20a}$$

$$\lambda_+^1 = r_o X_o \tag{20b}$$

which means that the solution associated with total extinction is a saddle point. Next, we consider eqs 12a and b and find

$$\lambda_-^2 = -r_o X_0 \tag{20c}$$

$$\lambda_+^2 = \frac{X_o(k-1)-1}{1+X_o} \tag{20d}$$

Here the predator extinction solution is a stable node if $X_o(k-1) < 1$, but a saddle point if $X_o(k-1) > 1$. Finally, in the case of (X_3^{ss}, Y_3^{ss}), we consider the trace and determinant of R,

$$\mathrm{tr}R = \frac{r_o}{\mathrm{k}}\left[X_o - \frac{k+1}{k-1}\right] \tag{21a}$$

$$\det R = \frac{r_o}{\mathrm{k}}\left[X_o(k-1)-1\right] \tag{21b}$$

Notice the similarity between eqs 13b–20d and eq 21b. As a consequence of this similarity, both the determinant of R and the steady state, Y_3^{ss}, associated with the prey–predator coexistence solution are negative when the predator extinction solution is stable, $X_o(k-1) < 1$. From our previous discussion, this means that while $(X_o, 0)$ is stable, the nonphysical coexistence solution is a saddle point. At $X_o = 1/(k-1)$, we get $\lambda_-^2 = -r_o X_o$ and $\lambda_+^2 = 0$, these parameter values define a saddle-node bifurcation, where both the predator extinction and coexistence solutions change their dynamic properties. Now, when $(X_o, 0)$ is a saddle point, the determinant of R associated with (X_3^{ss}, Y_3^{ss}) is positive, and we have several possibilities. First, we consider $4\det R < (\mathrm{tr}R)^2$, where a stable node is observed for the coexistence solution if the tr$R$ is negative and an unstable node if the tr$R$ is positive. Second, if $4\det R > (\mathrm{trR})^2$ we get two imaginary eigenvalues, and the stability is given solely by the tr$R$. One possibility is a stable focus or attractor showing damped oscillations. Another possibility is an unstable focus or repeller showing a limit cycle; therefore, we find again a change in dynamic behavior at tr$R$ = 0, which defines a second bifurcation in the MLVM.

To determine the second bifurcation we need to find a relation between the parameters that yields a zero trace. Using eq 21a, we find the following equivalent relations that yield a zero trace for the coexistence solution:

$$X_o = \frac{k+1}{k-1} \tag{22a}$$

$$k = \frac{X_o+1}{X_o-1} \tag{22b}$$

Now, if we consider parameter values near the bifurcation relation, most likely $(\mathrm{tr}R)^2$ will be less than $4\det R$, and we get two imaginary eigenvalues. Hence, we can select parameter values that will give us damped oscillations as well as stable limit cycles.

It is plausible after this analysis to pick parameter values such that $X_o(k-1) < 1$. This choice will yield a stable predator extinction solution and a nonphysical coexistence solution. Furthermore, we can select parameter values in the nearby neighborhood in parameter space such that $X_o(k-1) \approx> 1$, which gives us a saddle point for the predator extinction solution and a stable node for the coexistence solution. Finally, by changing the parameters, we can obtain damped and stable oscillations. In summary, the MLVM gives a plethora of dynamic behaviors closer to the dynamics observed in nonlinear chemical kinetics.

Numerical Results

Our analysis of the two-variable model, eqs 8a and 8b, occurs in several stages. In the first stage, we vary one parameter (k) while holding the other parameters constant (Table 1). Notice that the critical bifurcation values of k are given by eqs 20d–22b, k_c^{sn} = 1.1250, k_c^{uf} = 1.2857. For this case, we examine the effects of the parameter changes on X and Y in phase space, which is depicted in Figure 1. We start with $k = 1.01 < k_c^{sn} < k_c^{uf}$ and get a stable node for the predator extinction solution, (8, 0), and a saddle point for the

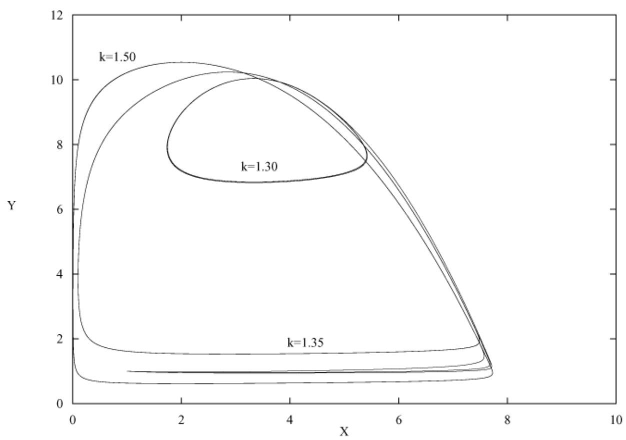

Figure 2. Effects of k on the amplitude of the oscillations in phase using parameters in Table 1 and different k values.

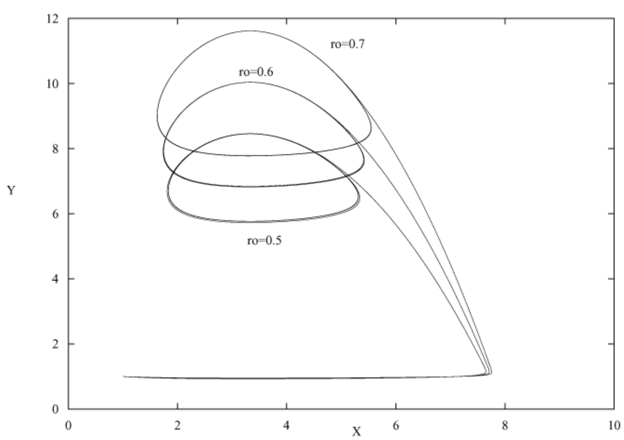

Figure 3. Effects of r_o on the amplitude of the oscillations in phase space for $X_o = 8.00$, $k = 1.30$, and different r_o values.

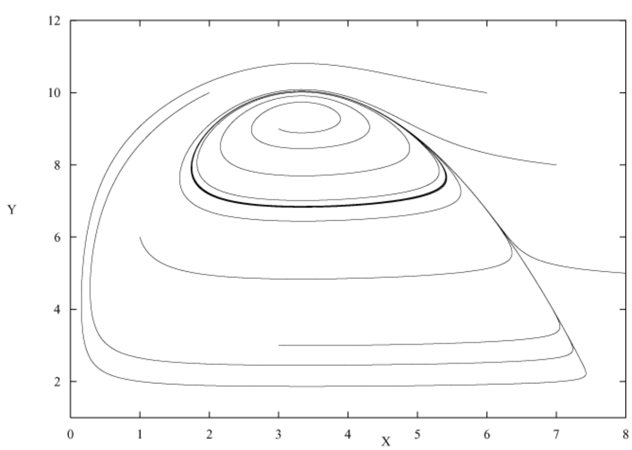

Figure 4. Examples of different trajectories in phase space for X_o = 8.00, $k = 1.30$, and $r_o = 0.60$, and different initial conditions.

Table 2. Dimensionless Values

Parameter	Value
r_o	= 0.60
k	= 1.30
X_o	≈ 8.00

nonphysical coexistence solution. As we change k to $k_c^{sn} < 1.20 < k_c^{uf}$, (8, 0) is a saddle point and (5, 9) is a stable node with two negative real eigenvalues, –1.262 and –0.238. Finally, we consider $k_c^{sn} < k_c^{uf} < k = 1.30$. In this case, the coexistence solution (9.33, 3.33) is an unstable focus and we find a limit cycle.

In Figure 2, we explore the effect of k on the oscillation's amplitude. As we can see, the amplitude increases as we increase the value of k. Parallel to this analysis, we change r_o instead of k in Figure 3, where we notice that amplitude increases as we increase r_o. To complement these observations, we consider $X_o = 8.00$, $r_o = 0.60$, and $k = 1.30$ in Figure 4, and we choose seven different initial conditions. Our choice is such that only one of those initial conditions spirals out towards the limit cycle, while the other six spiral in.

Next, we fix the value of k as in Table 2 and vary the value of the dimensionless carrying capacity, X_o. In Figure 5, we start with $X_o = 7.00$, which yields damped oscillations characteristic of a stable focus. Also showing damped oscillations is the value $X_o = 7.50$. For $X_o = 8.0$, as we have seen before, we get a limit cycle. Finally, we consider $X_o = 8.5$ and notice that the amplitude has increased as we increased X_o. As confirmation of this bifurcation we use eq 22a and find that the bifurcation value of X_o is equal to $X_o^{uf} = 7.666$, which is consistent with our numerical analysis.

In the last part of the numerical analysis, we considered some time series. For the previous parameter values, $X_o = 8.00$, $k = 1.30$, and $r_o = 0.60$, we depict the time series in Figure 6 where we can notice the transient oscillations from the initial condition to the stable limit cycle. In this particular case, the predator population is greater than the prey population at any time. As we change the values to $X_o = 8.00$, $k = 1.325$, and $r_o = 0.60$, the maximum value of Y is greater than the maximum of X. But, as we can see in Figure 7, now these maxima alternate in time. Finally, we consider a last set of parameter values, $X_o = 8.00$, $k = 1.325$, and $r_o = 0.30$, and depict the time series in Figure 8. In this case the maxima alternate in time, but now the maxima of Y is less than the maxima of X; therefore, the MLVM allow different shapes of oscillation that can be matched to any experimental observations

Discussion

In the previous sections we have introduced and analyzed a Modified Lotka–Volterra Model. For this model we have used a linear stability analysis to obtain dynamic properties of the steady-state solution. The algebra involved in the analysis is quite simple, and all the results and relations presented are easy to obtain with or without the help of a program like Mathematica [11]. Furthermore, we encourage the readers to reproduce our results without the help of any symbolic software package. The analytical information was corroborated by numerical integration of the ODEs using a couple of software packages, including Mathematica [11]. For the MLVM we have obtained a bifurcation relation, multiple steady states, stable and unstable nodes, and limit cycles. Also, by varying either k or X_o, we have shown transitions from a stable node to damped oscillations to stable oscillations and from a stable node to a saddle point. The present modifications to the LVM include two changes. In order to have physical steady states and a bifurcation from stable steady states to stable limit cycles, both modifications are needed. Here we

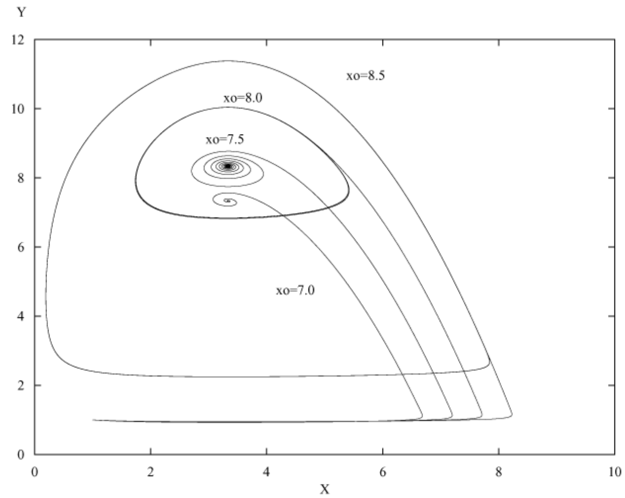

Figure 5. Phase-space representation of a transition through a bifurcation for the Modified Lotka–Volterra Model using parameters in Table 2 and different r_o values.

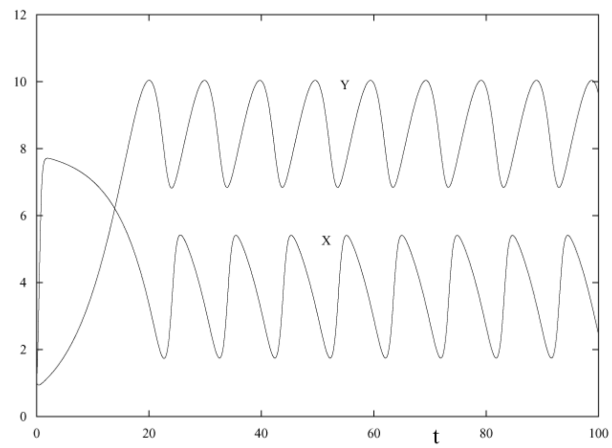

Figure 6. Time series of X and Y oscillation for $X_o = 8.00$, $k = 1.30$, and $r_o = 0.60$.

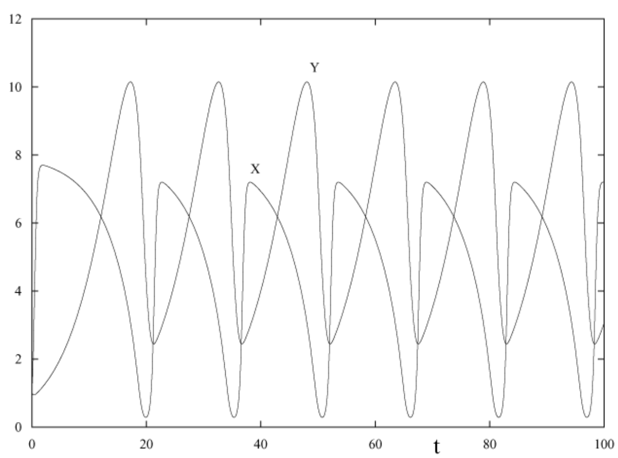

Figure 7. Time series of X and Y oscillation for $X_o = 8.00$, $k = 1.325$ and $r_o = 0.60$.

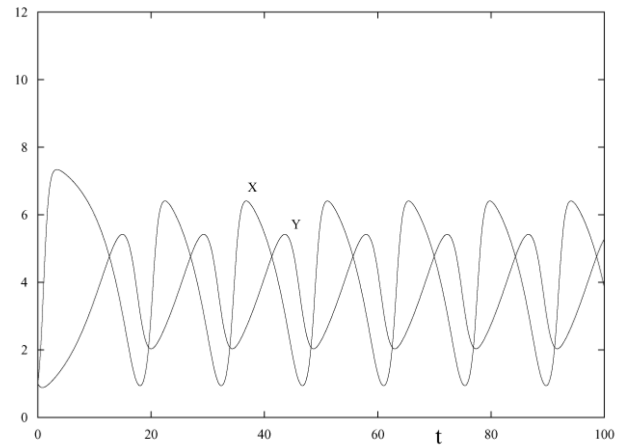

Figure 8. Time series of X and Y oscillation for $X_o = 8.00$, $k = 1.325$ and $r_o = 0.30$.

claim that each individual change cannot yield the latter changes in dynamic behavior. If one includes only a logistic growth of the prey, one finds that the eigenvalues are either pure real and negative or complex with a negative real part. Consequently, this change only shows stable nodes or a stable focus; that is, only damped oscillations are observed. The second modification alone cannot remove the fixed point at infinity. Also, the real part of the eigenvalues obtained are positive for any value of the parameters. It, therefore, cannot yield stable steady states, which are required for a bifurcation. Both of these results are left as exercises for the reader. In summary, the MLVM discussed in this paper gives an alternative to the LVM to introduce important concepts in nonlinear chemical kinetics. Not only does the MLVM show all the important dynamic properties as other popular chemical models [12–15], but also its study follows straightforward linear stability analysis, eliminating cumbersome and time-consuming algebra encountered in the analysis of other models [12–15].

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