The different trajectories obtained from the May-Holling-Tanner predator-prey model via numerical solutions

As diferentes trajetórias obtidas do modelo presa-predador de May-Holling-Tanner via soluções numéricas

Las diferentes trayectorias obtenidas del modelo presa-depredador de May-Holling-Tanner mediante soluciones numéricas

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ABSTRACT

Studies of the population dynamics of interactions between species modeled by systems of differential equations can help in the development of future scenarios capable of assisting in decision-making processes, such as biological control. The purpose of this work was to investigate the possible trajectories obtained from the ordinary differential equations of the May-Holling-Tanner predator-prey model, using numerical methods. For this, the two-step Adams-Moulton predictor-corrector method was adopted. Simulations of three scenarios were carried out, each of them varying the parameters of the model in study. The results showed that the parameter values have a great impact on the evolution of the populations, providing different trajectory profiles in the phase plan and that the chosen numerical method made it possible to generate satisfactory solutions.

Keywords: biomathematics, predator-prey model, May-Holling-Tanner, numerical methods.

RESUMO

O estudo de dinâmicas populacionais de interações entre espécies, modeladas via sistemas de equações diferenciais, pode auxiliar na investigação de futuros cenários e por conseguinte em processos de tomada de decisões, como por exemplo para controle biológico. O propósito deste trabalho foi examinar as possíveis trajetórias obtidas das equações diferenciais ordinárias do modelo do tipo presa-predador de May-Holling-Tanner, por meio de métodos numéricos.
Para isto, foi adotado o método de Adams-Moulton preditor-corrector de dois passos. Simulações de três cenários distintos foram realizadas, cada um deles variando os parâmetros do modelo em estudo. Os resultados mostraram que os valores dos referidos parâmetros têm grande impacto na evolução das populações, fornecendo diferentes perfis de trajetórias no plano de fase e que o método numérico escolhido possibilitou gerar soluções satisfatórias.

**Palavras-chave:** biomatemática, modelo presa-predador, May-Holling-Tanner, métodos numéricos.

**RESUMEN**

El estudio de la dinámica poblacional de las interacciones entre especies, modeladas mediante sistemas de ecuaciones diferenciales, puede ayudar en la investigación de escenarios futuros y por tanto en procesos de toma de decisiones, como por ejemplo para el control biológico. El propósito de este trabajo fue examinar las posibles trayectorias obtenidas a partir de las ecuaciones diferenciales ordinarias del modelo presa-depredador de May-Holling-Tanner, utilizando métodos numéricos. Para ello se adoptó el método predictor-corrector de dos pasos de Adams-Moulton. Se realizaron simulaciones de tres escenarios diferentes, variando cada uno de ellos los parámetros del modelo en estudio. Los resultados demostraron que los valores de los parámetros antes mencionados tienen un gran impacto en la evolución de las poblaciones, proporcionando diferentes perfiles de trayectoria en el plano de fases y que el método numérico elegido permitió generar soluciones satisfactorias.

**Palabras clave:** biomatemáticas, modelo depredador-presa, May-Holling-Tanner, métodos numéricos.

**1 INTRODUCTION**

Mathematical modeling and ordinary differential equations, combined with the advancement of numerical and computational techniques, have increasingly stood out for enabling studies of biological phenomena such as dynamics between populations and their consequences, through the simulation of different scenarios. Mathematical models are important because they allow you to predict future situations and help you make decisions.

A prominent interaction in biological systems is that which occurs between populations of prey and predators, and one of the mathematical models that can be used is the May-Holling-Tanner prey-predator system.
In this sense, the objective of this research was to investigate the different possible trajectories of the May-Holling-Tanner prey-predator mathematical model, through different numerical solutions, based on the references Buchanan (1992), Gasull (1997), Garcia and Silveira (2018) and Silveira and Garcia (2019, 2020). The importance of the May-Holling-Tanner model lies in the fact that it takes into account the predation effect and the support capabilities of prey and predator populations, which does not occur in the Lotka-Volterra model.

The reference Buchanan (1992) provides the basis for numerical studies of ordinary differential equations and the reference Gasull (1997) contains some values from the literature for the parameters of the May-Holling-Tanner system. The studies by Garcia and Silveira (2018) and Silveira and Garcia (2019, 2020) carried out comparisons of approximate solutions in biological systems via numerical methods of Euler, modified Euler, Classical Runge-Kutta, Adams-Bashforth of 2 steps and 4 steps and Adams-Moulton 2, with 2 steps and 4 steps, including the predictor-corrector technique. Therefore, the authors of this work chose to use the 2-step Adams-Moulton predictor-corrector method to obtain numerical solutions and their trajectories in the phase plan of the May-Holling-Tanner system, which models the dynamics of prey and predators.

Linking the different possible trajectories to the parameters of the May-Holling-Tanner prey-predator system, this work sought to analyze the impacts on the trajectory profile when considering variations in the values of the system parameters, and thus expand the studies carried out in Silveira and Garcia (2019, 2020).

In the next sections there are details of the mathematical model (Section 2), the chosen numerical method (Section 3) and the examples investigated (Section 4).

2 THE MAY-HOLLING-TANNER PREY-PREDATOR MODEL

The May-Holling-Tanner prey-predator model, or also called the Holling-Tanner type II model (Holling, 1959), emerged from the continuity of research on
population dynamics via the Leslie-Gower model (Leslie, 1948), whose ordinary differential equations are described by:

\[
\begin{align*}
\frac{dx}{dt} &= r x \left(1 - \frac{x}{K}\right) - \frac{mx}{A + x} y, \\
\frac{dy}{dt} &= s y \left(1 - \frac{c}{x} y\right), \\
\end{align*}
\]

where \(x(t)\) represents the prey population, \(y(t)\) corresponds to the predator population, \(r\) equals the birth rate of the prey population, \(K\) symbolizes the carrying capacity of the prey population, \(c\) is related to the amount of food needed to result in predator births and \(s\) is the birth rate of the predator population. In this system, a carrying capacity for the predator population is also considered, directly proportional to the amount of prey (based on the Leslie-Gower model), as well as the term known as response function \(-\frac{mx}{A + x} y\), based on the Michaelis-Menten model for concentrations of substances in enzymatic reactions (Cecconello; Silva; Bassanezi, 2012).

This model of interaction between species has some important characteristics:

- The population dynamics of prey follows the logistic model, with carrying capacity \(K\) and intrinsic ratio \(r\), in the absence of predators.
- The parameter \(m\) is the maximum number of prey that can be captured by the predator, per unit of time.
- The constant \(A\) refers to the prey’s ability to avoid attack by predators. It is observed that if the other parameters are kept constant, the higher \(A\) is, the smaller the influence of the predator on the prey population will be.
- The predator population grows logistically. The higher the \(\frac{y}{x}\) ratio, the smaller the number of prey available for each predator, and consequently, the predator population decreases.

To implement numerical studies, it is convenient to change the variables, \(\bar{t} = rt\), \(\bar{x} = \frac{x}{K}\) and \(\bar{y} = \frac{my}{rK}\) in system (1). Thus, after removing the slash notation
on the variables, we have the following equivalent system:

\[
\begin{align*}
\frac{dx}{dt} &= x(1-x) - \frac{x}{a+x} y, \quad x(0) = x_0 \quad e \quad y(0) = y_0. \\
\frac{dy}{dt} &= y \left( \frac{d}{a} - \frac{b}{x} y \right)
\end{align*}
\]  

(2)

The first equation of the system (2) can be rewritten as

\[
\frac{dx}{dt} = x(1-x) - f(x,a)y,
\]  

(3)

in which \( f = f(x,a) \) is called the response function, which in ecology is the ingestion rate of a predator (consumer) as a function of food density (prey density, that is, the amount of food available in one given ecotope), which influences the rate of reproduction of the predator population as a function of prey density.

The type II response function takes the form:

\[
f(x,a) = \frac{x}{a + x},
\]  

(4)

Where

\[ a > 0 \] is constant.

This response function has a hyperbolic profile and always slows down as food intake increases. Ecologically, this means that food processing by predators decreases, thus limiting predators' search for prey. Therefore, how much more predators feeding on prey, less the encounter between predators and prey will result in deaths and/or the predators stop looking for prey due to satiety and/or while they are feeding.

In this case the speed of the function \( f(x,a) \) is always positive, \( f'(x,a) > 0 \), and the acceleration is always negative, \( f''(x,a) > 0 \). Furthermore, high
numbers of prey saturate the number of predators, because the response function is limited and \( f(x, a) \to 1 \) when \( x \to \infty \).

The Figure 1 shows the response function curve. If \( x = a \), the response function takes the value \( f(a, a) = 0.5 \).

**Figure 1.** Response function of the Holling-Tanner type II model.

![Figure 1. Response function of the Holling-Tanner type II model.](image)

Source: Prepared by the authors themselves.

### 3 NUMERICAL METHODS

Consider the Initial Value Problem (IVP),

\[
\begin{align*}
x'(t) &= f(t, x), \quad t \in I \subseteq \mathbb{R} \\
x(0) &= x_0
\end{align*}
\]

(5)

Where

\[f: I \times \mathbb{R} \to \mathbb{R} \text{ and } x = x(t), x: I \to \mathbb{R}.\]

The discretization of the differential equation associated with the IVP (5) begins with the discretization of the temporal interval \( I \). Defining \( I = [0, t_f] \subseteq \mathbb{R} \), a regular partition of \( I \) is given by

\[\Pi : 0 = t_0 < t_1 < \cdots < t_i < t_{i+1} < \cdots < t_N = t_f\]
where \(N\) is the number of subintervals that partition \(I = [0, t_f]\), \(N + 1\) is the number of points that define the partition \(\Pi\) and \(h = \frac{t_f - t_0}{N}\) is the spacing between every two consecutive points, that is, \(h = t_{i+1} - t_i\), for \(i = 0, \cdots, N - 1\).

When specifying a numeric method, for each point \(t_i, i = 1, \cdots, N\), it is possible to determine an approximate value \(t_i\) for the analytical solution \(x_i = x(t_i)\) and the set \(\{x_0, x_1, \cdots, x_N\}\) is an approximate solution for IVP (5).

The numerical scheme chosen for this research was the two-step Adams-Moulton, with the predictor-corrector technique. For this scheme, conventional discretization was carried out and for an application of the same made use of the Adams-Bashforth 2 and modified-Euler methods. Below is a description of the methods following the references Buchanan (1992), Garcia and Silveira (2018), Silveira and Garcia (2020).

3.1 ADAMS-MOULTON 2 METHOD

In the implicit two-point, second-order Adams-Moulton scheme (also known as the implicit Trapezoidal method), the approximate solution \(\xi_{i+1}\) is

\[
\xi_{i+1} = \xi_i + \frac{h}{2} \left[f(t_{i+1}, \xi_{i+1}) + f(t_i, \xi_i)\right], \quad i = 0, \cdots, N - 1. \tag{6}
\]

Note that in this case it is not possible to obtain \(\xi_{i+1}\) recursively, making it necessary to solve a linear system defined by Equation (6). An alternative to avoiding solving the linear system is to use the concept of prediction and correction. The process consists of estimating \(\xi_{i+1}\) on the right side of the Equation (6), via some explicit method and replace it in the implicit method expression. In this way, the Adams-Moulton 2 predictor-corrector method, whose prediction is performed by the Adams-Bashforth 2 method, becomes
\[
\begin{aligned}
\xi_{\text{pred}} &= \xi_i + \frac{h}{2}[3f(t_i, \xi_i) + f(t_{i-1}, \xi_{i-1})], \\
\xi_{i+1} &= \xi_i + \frac{h}{2}[f(t_{i+1}, \xi_{\text{pred}}) + f(t_i, \xi_i)], \\
\end{aligned}
\]
\[i = 1, \ldots, N - 1. \tag{7}\]

### 3.2 Adams-Bashforth 2 and Modified Euler Methods

In the explicit two-point, second-order Adams-Bashforth scheme, the approximate solution \(\xi_{i+1}\) is defined by

\[
\xi_{i+1} = \xi_i + \frac{h}{2}[3f(t_i, \xi_i) + f(t_{i-1}, \xi_{i-1})], \quad i = 1, \ldots, N - 1. \tag{8}\]

Note that \(\xi_{i+1}\) is not defined in Equation (8), therefore it is necessary to obtain it by a simple step scheme. In this study, we opted for the modified Euler method defined by Equation (9):

\[
\begin{aligned}
m_1 &= f(t_i, \xi_i) \\
m_2 &= f(t_i + h, \xi_i + hm_1), \\
\xi_{i+1} &= \frac{h}{2}(m_1 + m_2), \\
\end{aligned}
\]
\[i = 0, \ldots, N - 1. \tag{9}\]

### 4 Computational Simulations

In this section, we will show the numerical simulations obtained taking into account data present in the references Gasull et al. (1997), Garcia and Silveira (2018), Silveira and Garcia (2019, 2020). The different possible trajectories, when varying the parameters \(a, b\) and \(d\) of the initial value problem, IVP (2), will be explored in the May-Holling-Tanner prey-predator system (2).

The own codes were created in a **GNU Octave - version 6.4.0**, configured by a **x86_64-pc-linux-gnu**, taking as a reference Quarteroni and Saleri (2017).

In all simulations, as seen in System (2), prey and predator populations were normalized with respect to the carrying capacity of each. Furthermore, the
blue curves represent prey populations, variable $x$; the red curves are the solutions for the predator population, variable $y$. In the phase plans, graphs of prey ($x$-axis) versus predators ($y$-axis), the black dot is the initial condition of prey and predators, $(x(0), y(0)) = (x_0, y_0) = (0.5, 0.5)$.

4.1 EXAMPLE 1 - PARAMETER VARIATION a

In this example, for population dynamics were set $b = 0.1$ and $d = 0.1$. In this way, simulations were carried out to $a = 0.01$, $a = 0.1$, $a = 0.2$, $a = 0.3$, $a = 0.4$, $a = 1.0$ and $a = 100$.

In all cases, the initial populations were considered $x(0) = x_0 = 0.5$ (prey), $y(0) = y_0 = 0.5$ (predators) and this point is represented in the phase plan graphs in black.

4.1.1 Parameters $a = 0.1$ and $a = 0.2$

In these simulations, the following were used for temporal discretization: initial time $t_0 = 0$, final time $t_f = 140$ and $h = 0.05$.

With the parameter $a = 0.1$, the simulations showed that, initially, prey and predator populations decrease, reaching close to 0.1; then the prey population grows rapidly and stabilizes near of the carrying capacity, while the predator population takes time to start growing, Figure 2-a. When the predator population increases, we can see the impact on the prey population which starts to decrease, Figure 2-a. Then the amount of prey is no longer enough to feed the predators, which leads to the number of predators also decreasing and both return to values close to zero, Figure 2-a. Finally, this dynamic repeats itself and populations enter into cyclical behavior, Figure 2-b. Consequently, the trajectory profile of this dynamic in the phase plan is that of a limit cycle, Figure 2-b and therefore, prey and predator populations keep oscillating, Figure 2-a. The minimum and maximum values of populations are approximately 0.9 and that of predators approaches 0.4.
In these examples, the first simulation was done with $t_0 = 0$, $t_f = 140$ and $h = 0.05$. When changing the parameter to $a = 0.2$, the change in the profile is immense. With the final time of $t_f = 140$, the exponential decay occurred, but it was not possible to verify whether the populations stabilize at some value. In this way, the final time was extended to $t_f = 300$ and, thus, both populations decay, stabilizing at $0.36$, Figure 3.

Figure 2. Evolution of prey and predator populations, respectively $x$ and $y$ in graph (a), and the phase plan - graph (b), with $a=0.1$.

![Graphs](image)

Source: Prepared by the authors themselves.

Figure 3. Extension to $t_f = 300$, with $a=0.2$.

![Graphs](image)

Source: Prepared by the authors themselves.
4.1.2 Parameters $a = 0.4$ and $a = 0.5$

In this dynamic, the same characteristics as the previous example remain, however, the equilibrium point is even closer to the initial condition point and the populations reach this equilibrium even faster, Figures 4-a and 4-b. Therefore, it was considered $t_f = 60$, with $h = 0.05$. When $a = 0.5$, populations already start at the equilibrium point, remaining constant over time, Figures 5-a and 5-b.

Figure 4. Evolution of prey and predator populations, respectively $x$ and $y$ in graph (a), and the phase plan - graph (b), with $a=0.4$.

![Figure 4](image1)

Source: Prepared by the authors themselves.

Figure 5. Evolution of prey and predator populations, respectively $x$ and $y$ in graph (a), and the phase plan - graph (b), with $a=0.5$.

![Figure 5](image2)

Source: Prepared by the authors themselves.
4.1.3 Parameters $a = 1$ and $a = 100$

From values to $a > 0.5$, the populational dynamics will have an equilibrium point greater than their initial values. In this example, both populations start growing, the prey population reaches a peak and then declines, stabilizing at approximately 0.62. Meanwhile, the predator population grows, with behavior similar to logistical growth limited by its carrying capacity, see Figure 6-a. The phase plan no longer has a spiral profile, becoming a curve that goes to its equilibrium point, Figure 6-b. In this simulation we used $t_f = 60$ and $h = 0.05$.

It is noted that when increasing the value of the parameter $a$ from one to two, the equilibrium point of the populations became closer to the point $(1, 1)$, Figure 7-b. This trend remains and when taking $a = 100$, the population equilibrium point becomes even closer to $(1, 1)$, Figures 7-a and 7-b.

Figure 6. Evolution of prey and predator populations, respectively x and y in graph (a), and the phase plan - graph (b), with a=1.
Figure 7. Evolution of prey and predator populations, respectively x and y in graph (a), and the phase plan - graph (b), with a=100.

(a)  (b)

Source: Prepared by the authors themselves.

4.2 EXAMPLE 2 - PARAMETER VARIATION d

In this subsection, the parameters set were \( a = 0.2 \) and \( b = 0.06 \). For the \( d \) parameter, the values 0.01, 0.05, 0.1, 0.2 and 0.3 were used. In all simulations, the initial values of the populations were \( x_0 = 0.5 \) and \( y_0 = 0.5 \).

4.2.1 Parameter \( d = 0.01 \)

With the value of \( d = 0.01 \) and with the adopted discretization of \( t_f = 200 \), with \( h = 0.05 \), the first simulation was carried out.

The populations of prey and predators start decreasing and, suddenly, there is a rapid increase in the prey population, which stabilizes at approximately 0.82, Figure 8-a. The growth of prey causes the decline of predators to decrease, causing this population to stabilize close to the value 0.18, Figure 8-a. The profile of this phase plan is an evolution that describes a curve, in the shape of a gain, that goes to the equilibrium point (0.82, 0.18), Figure 8-b.
Figure 8. Evolution of prey and predator populations, respectively x and y in graph (a), and the phase plan - graph (b), with d=0.01.

(a) ![Graph (a)](image1.png)

(b) ![Graph (b)](image2.png)

Source: Prepared by the authors themselves.

4.2.2 Parameters $d = 0.05$ and $d = 0.1$

In $d = 0.05$ scenario, the populations oscillate until reaching a point of equilibrium, Figure 9-a. Populations stabilize at different values, prey populations close to 0.42 and predator populations at 0.38, describing a trajectory in the form of a spiral in the phase plan, Figure 9-b.

Continuing with the variation of the $d$ parameter, the populations describe an oscillatory behavior, Figure 10-a, with a limit cycle trajectory, Figure 10-b, differentiating itself from previous cases.
4.2.3 Parameters $d = 0.2$ and $d = 0.3$

The simulation for $d = 0.2$ presented an oscillatory behavior in which the amplitudes of the prey and predator populations decrease, Figure 11-a. The result in the phase plan is a spiral trajectory, Figure 11-b. It is possible to see the exponential decay of populations and their respective stabilization at 0.25 for prey and 0.08 for predators.
Figure 11. Evolution of prey and predator populations, respectively $x$ and $y$ in graph (a), and the phase plan - graph (b), with $d=0.2$.

(a) \hspace{1cm} (b)

Source: Prepared by the authors themselves.

Figure 12. Evolution of prey and predator populations, respectively $x$ and $y$ in graph (a), and the phase plan - graph (b), with $d=0.3$.

(a) \hspace{1cm} (b)

Source: Prepared by the authors themselves.

To $d = 0.3$, the oscillatory behavior of the populations continues, however the exponential decay was much faster, Figures 12-a and 12-b, and the populations reached the equilibrium point.

4.3 EXAMPLE 3 - PARAMETER VARIATION $b$

In this subsection, the parameters $a$ and $d$ were fixed, $a = 0.2$ and $d = 0.2$, and simulations were performed for $b=0.01$, $b=0.05$, $b=0.1$, $b=0.2$ and $b=0.5$. For the initial populations there are $(0.5, 0.5)$ in all implemented scenarios.
The solution profile begins in the shape of a spiral, which quickly converges to the equilibrium point, where populations of prey and predators stabilize, Figures 13-a and 13-b. Afterwards, the profile becomes a spiral with several cycles, that is, the populations of prey and predators oscillate and the amplitudes of the populations decay exponentially, Figures 14-a and 14-b. Next, the profile is that of a limit cycle whose beginning of the temporal evolution behaves like a spiral, Figures 15-a and 15-b. The solutions return to the behavior of a spiral with $b = 0.2$, Figures 16-a and 16-b, and finally, the profile becomes a curve that quickly stabilizes at the equilibrium point, Figures 17-a and 17-b.

Figure 13. Evolution of prey and predator populations, respectively $x$ and $y$ in graph (a), and the phase plan - graph (b), with $b=0.01$.

![Figure 13](image1.png)

Source: Prepared by the authors themselves.

Figure 14. Evolution of prey and predator populations, respectively $x$ and $y$ in graph (a), and the phase plan - graph (b), with $b=0.05$.

![Figure 14](image2.png)

Source: Prepared by the authors themselves.
Figure 15. Evolution of prey and predator populations, respectively x and y in graph (a), and the phase plan - graph (b), with b=0.1.

(a) (b)

Source: Prepared by the authors themselves.

Figure 16. Evolution of prey and predator populations, respectively x and y in graph (a), and the phase plan - graph (b), with b=0.2.

(a) (b)

Source: Prepared by the authors themselves.
Figure 17. Evolution of prey and predator populations, respectively \( x \) and \( y \) in graph (a), and the phase plan - graph (b), with \( b=0.5 \).

(a) ![Graph showing the evolution of prey and predator populations](image)

(b) ![Phase plane showing the dynamics of prey and predator populations](image)

Source: Prepared by the authors themselves.

5 CONCLUSIONS

The purpose of this study was to investigate the different trajectories of prey and predator populations, by carrying out computer simulations combining different values adopted for the parameters of ordinary differential equations, described in the May-Holling-Tanner mathematical model. For this, the Adams-Moulton 2 predictor-corrector method was chosen to obtain approximate numerical solutions of the system of differential equations.

Simulations of three different scenarios were performed, varying the parameters \( a \), \( b \) and \( d \) of the prey-predator model, starting by taking values contained in the literature and obtaining numerical solutions and their respective trajectories in the phase plan. The results showed that, depending on the choice of parameters for the System (2), the dynamics of prey and predator populations have different behaviors.

In Example 1, the solutions had a limit cycle behavior, going through a spiral with limit cycle, spiral profiles, constant solution and a convergent curve towards the equilibrium point, depending on the value of \( a \) chosen.

The variations of the parameters \( b \) and \( d \), Examples 2 and 3, presented the same trajectory structures, but with different behavior profiles. Spirals with slow exponential decay and solutions that resemble the logistic growth profile...
were found.

In all numerical solutions implemented, the chosen numerical method was sufficient to obtain stable approximate solutions. Therefore, in this work it was possible to investigate variations in trajectory profiles, by making changes to the values of the parameters of the May-Holling-Tanner prey-predator model, highlighting viable scenarios within the approximate solutions obtained.
REFERENCES


