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**Chaos in a Hybrid Three-Species Food Chain with
Beddington-Deangelis Functional Response**

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In this paper, a hybrid three-species food-chain model with Beddington-DeAngelis functional response has been studied. Local stability of the equilibria described by this model have been proved. By means of computer simulations, the complex dynamics of the model, especially chaos, have been identified. Furthermore, the largest Lyapunov exponent has been used to demonstrate the chaotic dynamics.

Keywords: Chaos, Food chain, Beddington-DeAngelis functional response, the Largest Lyapunov exponent

1. Introduction

Various types of interaction can occur between two species, including Holling-I, Holling-II, Holling-III, Beddington-DeAngelis, and others. Two-species continuous-time models of interacting species have been proposed by many authors (Gutierrez et al., 1992; Holling et al., 1965; Leslie et al., 1960). However, the dynamic behaviors of these models are not complex: they exhibit dynamics only of steady states and of limit cycles. As a result, more and more researchers have begun to investigate three-species food-chain models (Gakkhar et al., 2003; Gakkhar et al., 2006; Gakkhar et al., 2007; Hastings et al., 1991; Lv et al., 2008; Wang et al., 2008; Zhao et al., 2009a) and have found rich dynamics, including limit cycles, quasi-periodic behavior, and chaos. Especially in models of the Leslie-Gower type (Nindjin et al., 2008; Wang et al., 2008), chaos is frequently observed.

In the past few years, some authors have investigated a class of semi-ratio-dependent predator-prey systems, as described by the following equations:

$$\begin{cases} \frac{dx}{dt} = r_1 x(t) - a_1 x(t)^2 - c(x)y(t) \\ \frac{dy}{dt} = r_2 y(t) - \frac{d_1 y(t)^2}{x(t)} \end{cases}$$

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Recently, Wang and Pang investigated a hybrid ratio-dependent three-species food-chain model, which can be described as:

$$\begin{cases} \frac{dx}{dt} = r_1x(t) - a_1x(t)^2 - c(x)y(t) \\ \frac{dy}{dt} = r_2y(t) - \frac{d_1y(t)^2}{x(t)} - F(y)z(t), \\ \frac{dz}{dt} = kF(y)z(t) - d_2z(t) \end{cases}$$

where $c(x) = a_2x(t)$, $F(y) = by(t)/(\delta + y(t))$.

They investigated the persistence and Hopf bifurcations of the system and carried out computer simulations to support their conclusions.

In this paper, the authors report on a three-species food-chain model which can be described by the following system:

$$\begin{cases} \frac{dx}{dt} = r_1x \frac{g_0 - x}{g_1 - x} - \frac{a_1xy}{x + k_1} \\ \frac{dy}{dt} = r_2y - \frac{a_2y^2}{x + k_2} - \frac{byz}{c + y + ez}, \\ \frac{dz}{dt} = \frac{b_1yz}{c + y + ez} - d_2z \end{cases} \tag{1.1}$$

where $r_1, r_2, g_0, g_1, a_1, a_2, k_1, k_2, b, c, e, b_1$, and d_2 are positive constants, r_1, r_2 represent the intrinsic growth rate of the prey x and the intermediate predator y respectively, r_1g_0 represents the carrying capacity, g_1 is the limiting value of available resources, $a_1xy/(x + k_1)$ is Holling-II function response, $a_2y^2/(x + k_2)$ is the modified Leslie-Gower scheme, $byz/(c + y + ez)$ and $b_1yz/(c + y + ez)$ are the Beddington-DeAngelis functional response, and d_2 is the death rate of the top predator z . Because of its biological significance, the state space of system (1.1) will be defined as: $R_+^3 = \{(x, y, z) \mid x \geq 0, y \geq 0, z \geq 0\}$.

2. Local stability of equilibria

In the following discussion, the Jacobean matrix is used to analyze the local stability of system (1.1).

(1) The Jacobean matrix of system (1.1) at the equilibrium point $E_0 = (0, 0, 0)$ is:

$$J(0, 0, 0) = \begin{pmatrix} \frac{r_1g_0}{g_1} & a & 0 \\ 0 & r_2 & 0 \\ 0 & 0 & -d_2 \end{pmatrix}.$$

The roots of the characteristic equation of $J(0, 0, 0)$ are $\lambda_1 = r_1g_0/g_1 > 0$, $\lambda_2 = r_2 > 0$, and $\lambda_3 = -d_2 < 0$, and therefore $E_0 = (0, 0, 0)$ is a saddle point.

(2) The Jacobean matrix of system (1.1) at the equilibrium point $E_1 = (g_0, 0, 0)$ is:

$$J(g_0, 0, 0) = \begin{pmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{pmatrix},$$

with

$$a_{11} = (r_1g_0^2k_1^2 + 2r_1g_0^3k_1 - r_1g_0^3g_1 - r_1g_0g_1k_1 + r_1g_0^4)/(g_0 - g_1)^2, a_{12} = -a_1g_0/(g_0 + k_1), a_{13} = 0, a_{21} = 0, a_{22} = (r_2k_2c^2 + r_2g_0c^2)/((g_0 + k_2)c^2), a_{23} = 0, a_{31} = 0, a_{32} = 0, \text{ and } a_{33} = -d_2.$$

Because $\lambda_2 = (r_2k_2c^2 + r_2g_0c^2)/((g_0 + k_2)c^2) > 0$, so $E_1 = (g_0, 0, 0)$ is a saddle point.

(3)The equilibrium point $E_3 = (x^*, y^*, 0)$ can be analyzed in terms of a subsystem of the equations in system (1.1):

$$\begin{cases} \frac{dx}{dt} = r_1 \frac{g_0 - x}{g_1 - x} - \frac{a_1xy}{x + k_1} \\ \frac{dy}{dt} = r_2y - \frac{a_2y^2}{x + k_2} \end{cases} \tag{2.1}$$

When system (1.1) is limited to the (x, y) plane, clearly $E_3 = (x^*, y^*, 0)$ exhibits the same behavior as $E_{31} = (x^*, y^*)$, which is a non-negative equilibrium point of subsystem (2.1). The Jacobean matrix of subsystems (2.1) at $E_{31} = (x^*, y^*)$ is:

$$J(x^*, y^*) = \begin{pmatrix} G_{11} & G_{12} \\ G_{21} & G_{22} \end{pmatrix},$$

where

$$G_{11} = (-2r_1g_1x^{*3} + 2r_1k_1x^{*3} + r_1k_1^2x^{*2} + 2r_1g_0g_1k_1x^* + r_1x^{*4} + r_1g_0g_1x^{*2} + r_1g_0g_1k_1^2 - 4r_1g_1k_1x^{*2} - 2r_1g_1k_1^2x^* - a_1g_1^2k_1y^* - a_1k_1x^{*2}y^* + 2a_1g_1k_1x^*y^*)/(-g_1 + x^*)^2(x^* + k_1)^2, G_{12} = -a_1x^*/(x^* + k_1); G_{21} = a_2y^{*2}/(x^* + k_2)^2; G_{22} = (r_2x^* - 2a_2y^* + r_2k_2)/(x^* + k_2).$$

The characteristic equation of $J(x^*, y^*)$ is $\lambda^2 + \delta_1\lambda + \delta_2 = 0$, where $\delta_1 = -(G_{11} + G_{22})$, $\delta_2 = G_{11}G_{22} - G_{12}G_{21}$. According to the Routh-Hurwitz criterion, $E_{31} = (x^*, y^*)$ is locally and asymptotically stable if and only if $\delta_i > 0(i = 1, 2)$.

(4)The Jacobean matrix of system (1.1) at the equilibrium point $E_5 = (x^*, y^*, z^*)$ is:

$$J_3 = \begin{pmatrix} H_{11} & H_{12} & H_{13} \\ H_{21} & H_{22} & H_{23} \\ H_{31} & H_{32} & H_{33} \end{pmatrix}.$$

where

$$H_{11} = (r_1k_1x^{*2} + 2r_1k_1x^{*3} - 2r_1g_1x^{*3} - a_1k_1x^{*2}y^* - a_1k_1g_1^2y^* - 2r_1g_1k_1^2x^* - 4r_1g_1k_1x^{*2} + r_1g_0g_1k_1 + r_1g_0g_1x^{*2} + r_1x^{*4} + 2r_1g_0g_1k_1x^* + 2a_1g_1k_1x^*y^*)/(-g_1 + x^*)^2(x^* + k_1)^2, H_{22} = (-bek_2z^{*2} - bk_2cz^* - bex^*z^{*2} - 2a_2e^2y^*z^{*2} - 4a_2ey^{*2}z^* + r_2k_2e^2z^{*2} + 2r_2k_2cy^* + r_2e^2x^*z^{*2} + 2r_2cx^*y^* + 2r_2ex^*y^*z^* + 2r_2k_2cez^* + 2r_2k_2ey^*z^* - 2a_2y^{*3} - 4a_2y^{*3} - 4a_2cey^*z^* - 4a_2cy^{*2} - 2a_2c^2y^* + r_2k_2y^{*2} + r_2k_2c^2 + r_2x^*y^{*2} + r_2c^2x^* + 2r_2cex^*z^*)/(x^* + k_2)(c + y^* + ez^*)^2, H_{12} = -a_1x^*/(x^* + k_1) < 0; H_{13} = 0; H_{21} = a_2y^{*2}/(x^* + k_2) > 0; H_{23} = -by^*(c + y^*)/(c + y^* + ez^*)^2 < 0; H_{31} = 0; H_{32} = b_1z^*(c + ez^*)/(c + y^* + ez^*)^2 > 0; H_{33} = (-b_1y^*c - b_1y^2 + d_2c^2 + 2d_2cy^* + 2d_2cez^* + d_2y^{*2} + 2d_2e_1z^* + d_2e_1^2z^{*2})/(c + y^* + ez^*)^2.$$

The characteristic equation of $J(x^*, y^*, z^*)$ is $\lambda^3 + \sigma_1\lambda^2 + \sigma_2\lambda + \sigma_3 = 0.$, where

$$\sigma_1 = -(H_{11} + H_{22} + H_{33}), \quad \sigma_2 = H_{11}H_{22} - H_{12}H_{21} - H_{23}H_{32} + H_{11}H_{33},$$

$$\sigma_3 = H_{11}H_{23}H_{32} - H_{11}H_{22}H_{33} + H_{12}H_{21}H_{33}.$$

By the Routh-Hurwitz criterion, $E_2 = (x^*, y^*, z^*)$ is locally and asymptotically stable if and only if $\sigma_1 > 0, \sigma_3 > 0, \sigma_1\sigma_2 > \sigma_3$.

3. Numerical analysis

In this section, the global dynamic behaviors of the model are investigated by numerical simulation.

3.1. Bifurcation analysis

Figure 1 shows the bifurcation diagram of system (1.1) for successive maxima of species y and z . Here, successive maxima of y and z are plotted as functions of the bifurcation parameter g_0 . The interval of variation of g_0 is $3 \leq g_0 \leq 6.5$.

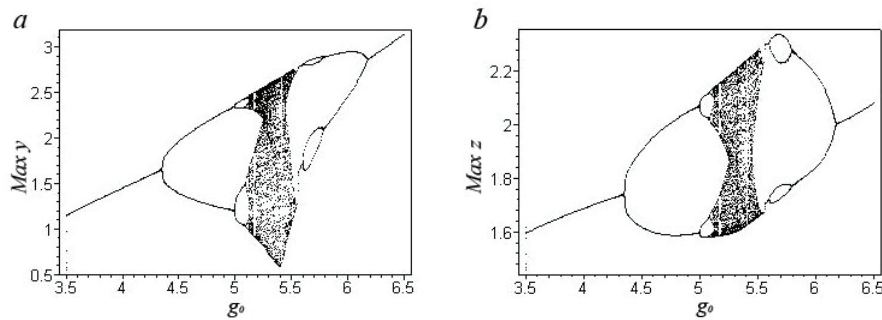


Figure 1. Bifurcation diagram of system (1.1): (a) maxima for species y ; (b) maxima for species z .

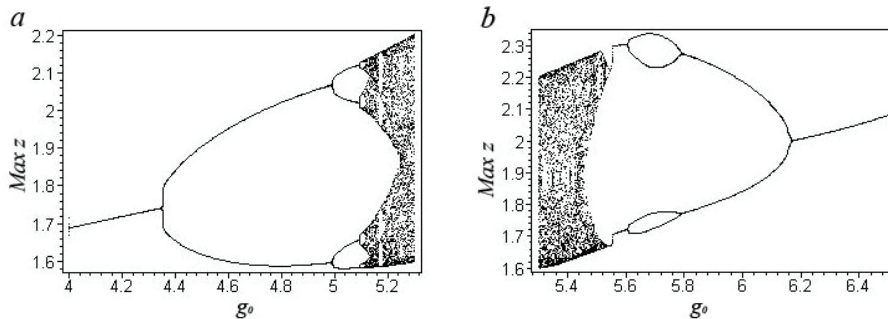


Figure 2. Magnified version of Figure 1 (b): (a) $4 \leq g_0 \leq 5.3$; (b) $5.3 \leq g_0 \leq 6.5$.

To see the dynamics of the system more clearly, the diagram must be magnified. Because the two diagrams are similar, only Figure 1(b) is magnified and shown in Figure 2. Figure 2 clearly shows the rich dynamics of the system, such as period-halving bifurcations and chaotic bands with periodic windows.

Figure 3 shows the bifurcation diagram of system (1.1) for successive maxima of species y and z too. But here, successive maxima of y and z are plotted as functions of the bifurcation parameter r_1 .

The interval of variation of r_1 is $1 \leq r_1 \leq 3.5$.

To see the dynamics of the system clearly, Figure 3(b) is magnified and shown in Figure 4. Figure 4 clearly shows the rich dynamics of the system, such as period-doubling bifurcations and chaotic bands with periodic windows.

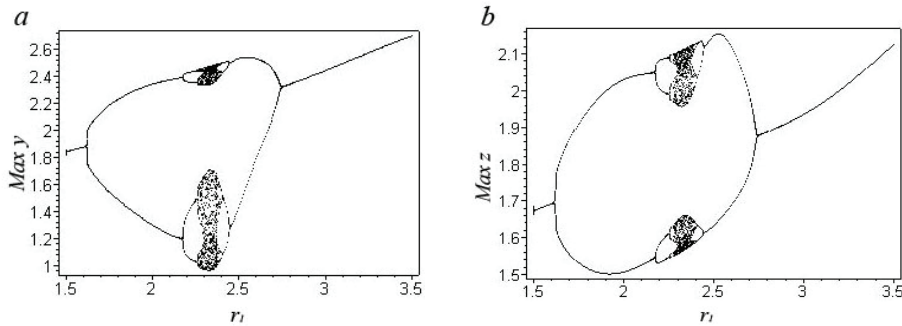


Figure 3. Bifurcation diagram of system (1.1): (a) maxima for species y ; (b) maxima for species z .

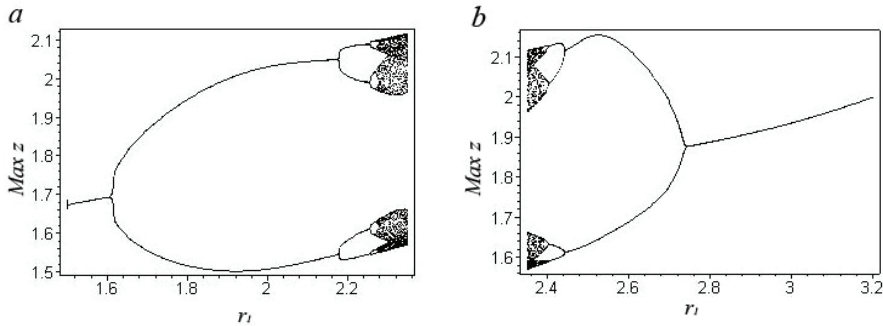


Figure 4. Magnified version of Figure 3 (b) : (a) $1.5 \leq r_1 \leq 2.35$; (b) $2.35 \leq r_1 \leq 3.2$.

3.2. The largest Lyapunov exponent

The largest Lyapunov exponent is used in this model to demonstrate the existence of chaos. The largest Lyapunov exponent is supposed to be the best quantitative measure of chaotic behavior(Zhao et al.,2009b; Zhao et al.,2009c). If the dynamics of the system are chaotic, then the largest Lyapunov exponent λ is positive. If they are periodic, then λ is negative. By plotting separately the largest Lyapunov exponent with respect to the two parameters r_1 g_0 (Figure 5), the chaotic behavior of the system can clearly be seen.

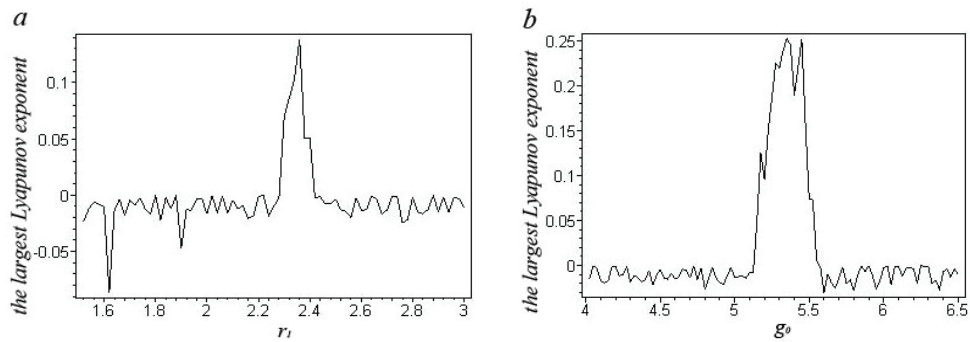


Figure 5. (a) The largest Lyapunov exponent of system (1.1) as a function of parameter r_1 : $1.5 \leq r_1 \leq 3$; (b) The largest Lyapunov exponent of system (1.1) as a function of parameter g_0 : $4 \leq g_0 \leq 6.5$.

4. Conclusions

This research has revealed the rich dynamic behaviors of a three-species food-chain model, including chaotic bands with periodic windows, period-doubling bifurcations, period-halving bifurcations, and chaos. From the bifurcation diagram, it is apparent that the system is sensitive to the values of the bifurcation parameters. The model also reveals that the system is particularly sensitive to the carrying capacity of the environment. Using the methods—the largest Lyapunov exponent, the chaotic behavior of the system is demonstrated.

Acknowledgements

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