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Research Article

Dynamic Behavior of a Commensalism Model with Nonmonotonic Functional Response and Density-Dependent Birth Rates

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In this paper, we propose and analyze a commensalism model with nonmonotonic functional response and density-dependent birth rates. The model can have at most four nonnegative equilibria. By applying the differential inequality theory, we show that each equilibrium can be globally attractive under suitable conditions. However, commensalism can be established only when resources for both species are large enough.

1. Introduction

Commensalism is a long-term biological interaction in which members of one species gain benefits while those of the other species neither benefit nor are harmed. An example of it is that remora are specially adapted to attach themselves to larger fish that provide locomotion and food. In the last decades, commensalism has attracted the attention of many researchers ([1–16]). Complicated dynamics have been found in the study. For example, in [3], Lin considered the effects of partial closure and harvesting. Depending on the size of the harvesting area, species can go extinct, partially survive, or become permanent. He also showed in [4] that the final density of the species increases as the Allee effect increases. This is quite different from results for predator-prey system with Allee effect.

Recently, Chen and Wu [5] proposed the following two species commensal symbiosis models with nonmonotonic functional response:

$$\frac{dx}{dt} = x\left(a_1 - b_1 x + \frac{c_1 y}{d_1 + y^2}\right), \qquad \frac{dy}{dt} = y\left(a_2 - b_2 y\right), \tag{1}$$

where $a_1, b_1, c_1, d_1, a_2, b_2$ are all positive constants. System (1) admits four nonnegative equilibria, $A_0(0,0)$, $A_1(a_1/b_1, 0)$, $A_2(0, a_2/b_2)$, and $A_3(x^*, y^*)$, where

$$x^* = \frac{a_1 b_2^2 d_1 + a_1 a_2^2 + a_2 b_2 c_1}{b_1\left(b_2^2 d_1 + a_2^2\right)}, \qquad y^* = \frac{a_2}{b_2}. \tag{2}$$

The stability of the equilibria is summarized as follows (see Theorem 2.1 and 2.2 in [5] for more detail).

Theorem A. *$A_0(0,0)$, $A_1(a_1/b_1, 0)$, and $A_2(0, a_2/b_2)$ are unstable; $A_3(x^*, y^*)$ is globally asymptotically stable.*

When the interaction between the species is ignored, the growth for both species is described by traditional logistic equations. Indeed, without the presence of y, the growth of the first species takes the form

$$\frac{dx}{dt} = x\left(a_1 - b_1 x\right), \tag{3}$$

where a_1 is the intrinsic growth rate and b_1 is the density-dependent coefficient or the interspecific competition coefficient. However, in most situations, the intrinsic growth rate is not always constant. One model incorporating nonconstant intrinsic growth rate is the following density-dependent model:

$$\frac{dx}{dt} = x\left(\frac{a_{11}}{a_{12} + a_{13}x} - a_{14} - b_1 x\right). \tag{4}$$

For more details, see [6–8]. Combining this with (1), we propose the following commensalism model:

$$\begin{aligned} \frac{dx}{dt} &= x\left(\frac{a_{11}}{a_{12} + a_{13}x} - a_{14} - b_1 x + \frac{c_1 y}{d_1 + y^2}\right), \\ \frac{dy}{dt} &= y\left(\frac{a_{21}}{a_{22} + a_{23}y} - a_{24} - b_2 y\right), \end{aligned} \tag{5}$$

where a_{ij} $(i = 1, 2, j = 1, 2, 3, 4)$ and b_1, c_1, d_1, and b_2 are all positive constants. Here $x(t)$ and $y(t)$ are the densities of the first and second species at time t, respectively. a_{11} and a_{21} stand for the total resources available per-unit-time for species x and y, respectively.

The aim of this paper is to investigate the attractivity of equilibria of (5). The main tool is the differential inequality theory or comparison principle. To the best of our knowledge, this is the first time to use differential inequality in this direction for ecosystems. The rest of the paper is arranged as follows. In Section 2, we obtain the existence and global attractivity of equilibria of system (5). Section 3 is devoted to illustrating the feasibility of the main results through numeric simulations. We end this paper by a brief discussion.

2. The Main Result

We first consider the existence of equilibria of (5). An equilibrium of (5) satisfies the equilibrium equations,

$$x\left(\frac{a_{11}}{a_{12} + a_{13}x} - a_{14} - b_1 x + \frac{c_1 y}{d_1 + y^2}\right) = 0, \tag{6}$$

$$y\left(\frac{a_{21}}{a_{22} + a_{23}y} - a_{24} - b_2 y\right) = 0. \tag{7}$$

If $a_{21} \le a_{22}a_{24}$ then (7) only has the unique nonnegative solution $y = 0$ while if $a_{21} > a_{22}a_{24}$, then, besides $y = 0$, (7) also has a unique positive solution $y^* = (-(a_{24}a_{23} + a_{22}b_2) + \sqrt{(a_{24}a_{23} + a_{22}b_2)^2 + 4b_2a_{23}(a_{21} - a_{22}a_{24})})/2b_2a_{23}$. Substituting $y = 0$ into (6), we see that if $a_{11} \le a_{12}a_{14}$, then $x = 0$ is the only nonnegative solution while if $a_{11} > a_{12}a_{14}$, besides $x = 0$, (6) also has a unique positive solution $x^* = (-(a_{14}a_{13} + a_{12}b_1) + \sqrt{(a_{14}a_{13} + a_{12}b_1)^2 + 4b_1a_{13}(a_{11} - a_{12}a_{14})})/2b_1a_{13}$. Similarly, substituting $y = y^*$ into (6), we can get that $x = 0$ is the only nonnegative solution if $a_{11} \le a_{12}a_{14}^*$ while, besides $x = 0$, (6) also has a unique positive solution $x^{**} = (-(a_{14}^*a_{13} + a_{12}b_1) + \sqrt{(a_{14}^*a_{13} + a_{12}b_1)^2 + 4b_1a_{13}(a_{11} - a_{12}a_{14}^*)})/2b_1a_{13}$ if $a_{11} > a_{12}a_{14}^*$, where $a_{14}^* = a_{14} - c_1y^*/(d_1 + (y^*)^2)$. In summary, we have obtained the following result.

Proposition 1. *The following statements on equilibria of (5) are valid.*

(i) *If $a_{11} \le a_{12}a_{14}$ and $a_{21} \le a_{22}a_{24}$ then there is only the trivial equilibrium $A_0 = (0, 0)$.*

(ii) *If $a_{11} > a_{12}a_{14}$ and $a_{21} \le a_{22}a_{24}$ then, besides A_0, there is also the nontrivial boundary equilibrium $A_1 = (x^*, 0)$.*

(iii) *If $a_{21} > a_{22}a_{24}$ and $a_{11} \le a_{12}a_{14}^*$ then there are only the two equilibria A_0 and $A_2(0, y^*)$.*

(iv) *If $a_{21} > a_{22}a_{24}$ and $a_{12}a_{14}^* < a_{11} \le a_{12}a_{14}$ then there are only three equilibria A_0, A_2, and $A_3(x^{**}, y^*)$.*

(v) *If $a_{21} > a_{22}a_{24}$ and $a_{11} > a_{12}a_{14}$ then there are only four equilibria A_0, A_1, A_2, and A_3.*

Before analyzing the stability of the equilibria of (5), we first consider the dynamic behavior of the following equation:

$$\frac{dy}{dt} = y\left(\frac{a_{21}}{a_{22} + a_{23}y} - a_{24} - b_2 y\right) \tag{8}$$

with $y(0) = y_0 \in [0, +\infty)$. Clearly, every such solution of (8) is nonnegative.

Lemma 2. *The following statements on (8) hold.*

(i) *If $a_{21} > a_{22}a_{24}$ then the unique positive equilibrium y^* is globally attractive in $(0, +\infty)$.*

(ii) *If $a_{21} \le a_{22}a_{24}$ then the equilibrium $y = 0$ is globally attractive in $[0, +\infty)$.*

Proof. Denote

$$F(y) = \frac{a_{21}}{a_{22} + a_{23}y} - a_{24} - b_2 y. \tag{9}$$

Note that

$$F(y) = \frac{-b_2a_{23}y^2 - (a_{24}a_{23} + a_{22}b_2)y + (a_{21} - a_{22}a_{24})}{a_{22} + a_{23}y}. \tag{10}$$

(i) When $a_{21} > a_{22}a_{24}$, it is easy to see that F only has the unique positive zero y^*. Observe that $yF(y) > 0$ for $y \in (0, y^*)$ and $yF(y) < 0$ for $y > y^*$. It follows easily that $\lim_{t\to+\infty} y(t) = y^*$ if $y_0 > 0$; that is, y^* is globally attractive in $(0, +\infty)$.

(ii) When $a_{21} \le a_{22}a_{24}$, clearly F can not have positive zero and hence $y = 0$ is the only equilibrium. As $yF(y) < 0$ for $y > 0$, we obtain $\lim_{t\to+\infty} y(t) = 0$. This completes the proof. □

Now we are ready to study the attractivity of the equilibria of (5).

Theorem 3. *(i) Assume that $a_{21} \le a_{22}a_{24}$ and $a_{11} < a_{12}a_{14}$. Then A_0 is globally attractive in $[0, +\infty) \times [0, +\infty)$.*

(ii) Suppose that $a_{21} \le a_{22}a_{24}$ and $a_{11} > a_{12}a_{14}$. Then A_1 is globally attractive in $(0, +\infty) \times [0, +\infty)$.

(iii) Assume that $a_{21} > a_{22}a_{24}$ and $a_{11} < a_{12}a_{14}^*$. Then A_2 is globally attractive in $[0, +\infty) \times (0, +\infty)$.

(iv) Assume that $a_{21} > a_{22}a_{24}$ and $a_{11} > a_{12}a_{14}^*$. Then the unique positive equilibrium A_3 is globally attractive in $(0, +\infty) \times (0, +\infty)$.

Proof. First, assume that $a_{21} \le a_{22}a_{24}$. By Lemma 2 (ii), we have $\lim_{t\longrightarrow+\infty} y(t) = 0$ for $y_0 \in [0,+\infty)$.

(i) As $a_{11} < a_{12}a_{14}$, we can choose $\varepsilon > 0$ small enough so that $a_{11} < a_{12}(a_{14} - c_1\varepsilon/d_1)$. For this ε, there exists $T_1 \ge 0$ such that $y(t) < \varepsilon$ for $t \ge T_1$. This, together with the first equation of (5), gives

$$\frac{dx}{dt} \le x\left(\frac{a_{11}}{a_{12}+a_{13}x} - a_{14} - b_1 x + \frac{c_1\varepsilon}{d_1}\right) \quad \text{for } t \ge T_1. \tag{11}$$

It follows from the choice of ε, Lemma 2 (ii), and the comparison principle that $\lim_{t\longrightarrow+\infty} x(t) = 0$. Therefore, $\lim_{t\longrightarrow+\infty}(x(t), y(t)) = A_0$; that is, A_0 is globally attractive in $[0,+\infty)\times[0,+\infty)$.

(ii) On the one hand, for any $\varepsilon > 0$ such that $a_{14}(\varepsilon) = a_{14} - c_1\varepsilon/d_1 > 0$, there exists $T_\varepsilon \ge 0$ such that $y(t) < \varepsilon$ for $t \ge T_1$. Thus it follows from the first equation of (5) that

$$\frac{dx}{dt} \le x\left(\frac{a_{11}}{a_{12}+a_{13}x} - a_{14}(\varepsilon) - b_1 x\right) \quad \text{for } t \ge T_\varepsilon. \tag{12}$$

Note that $a_{11} > a_{12}a_{14} > a_{12}a_{14}(\varepsilon)$. By comparison principle and Lemma 2 (i),

$$\limsup_{t\longrightarrow+\infty} x(t) \le x^*(\varepsilon) = \frac{-\left(a_{14}(\varepsilon)a_{13} + a_{12}b_1\right) + \sqrt{\left(a_{14}(\varepsilon)a_{13} + a_{12}b_1\right)^2 + 4b_1a_{13}\left(a_{11} - a_{12}a_{14}(\varepsilon)\right)}}{2b_1a_{13}}. \tag{13}$$

Letting $\varepsilon \longrightarrow 0^+$ gives $\limsup_{t\longrightarrow+\infty} x(t) \le x^*$. On the other hand, note that

$$\frac{dx}{dt} \ge x\left(\frac{a_{11}}{a_{12}+a_{13}x} - a_{14} - b_1 x\right). \tag{14}$$

Again, by comparison principle and Lemma 2 (i), we have $\liminf_{t\longrightarrow+\infty} x(t) \ge x^*$. It follows that $\lim_{t\longrightarrow+\infty} x(t) = x^*$. In summary, $\lim_{t\longrightarrow+\infty}(x(t), y(t)) = A_1$; namely, A_1 is globally attractive in $(0,+\infty)\times[0,+\infty)$.

Now suppose that $a_{21} > a_{22}a_{24}$. Then $\lim_{t\longrightarrow+\infty} y(t) = y^*$ for $y_0 > 0$ by Lemma 2 (i).

(iii) Since $a_{11} < a_{12}a_{14}^*$, we choose $\varepsilon > 0$ sufficiently small so that $a_{11} < a_{12}a_{14}^*(\varepsilon)$, where $a_{14}^*(\varepsilon) = a_{14} - c_1(y^* + \varepsilon)/(d_1 + (y^* - \varepsilon)^2)$. For this ε, there exists $\widehat{T}_\varepsilon \ge 0$ such that

$$y^* - \varepsilon < y(t) < y^* + \varepsilon \quad \text{for } t \ge \widehat{T}_\varepsilon. \tag{15}$$

This, combined with the first equation of (5), gives

$$\frac{dx}{dt} \le x\left(\frac{a_{11}}{a_{12}+a_{13}x} - a_{14}^*(\varepsilon) - b_1 x\right) \quad \text{for } t \ge \widehat{T}_\varepsilon. \tag{16}$$

Then $\lim_{t\longrightarrow+\infty} x(t) = 0$ by the choice of ε, Lemma 2 (ii), and the comparison principle. Thus we have shown $\lim_{t\longrightarrow+\infty}(x(t), y(t)) = A_2$; that is, A_2 is globally attractive in $[0,+\infty)\times(0,+\infty)$.

(iv) This time $a_{11} > a_{12}a_{14}^*$. For any $\varepsilon > 0$ such that $\widehat{a}_{14}^* = a_{14} - c_1(y^* + \varepsilon)/(d_1 + (y^* - \varepsilon)^2) > 0$ and $a_{11} > a_{12}\widetilde{a}_{14}^*(\varepsilon)$, there exists $\widetilde{T}_\varepsilon \ge 0$ such that

$$y^* - \varepsilon < y(t) < y^* + \varepsilon \quad \text{for } t \ge \widetilde{T}_\varepsilon, \tag{17}$$

where $\widetilde{a}_{14}^*(\varepsilon) = a_{14} - c_1(y^* - \varepsilon)/(d_1 + (y^* + \varepsilon)^2)$. Again, employing the first equation of (5), we have

$$\begin{aligned} x\left(\frac{a_{11}}{a_{12}+a_{13}x} - \widetilde{a}_{14}^*(\varepsilon) - b_1 x\right) &\le \frac{dx}{dt} \\ &\le x\left(\frac{a_{11}}{a_{12}+a_{13}x} - \widehat{a}_{14}^*(\varepsilon) - b_1 x\right) \end{aligned} \tag{18}$$

for $t \ge \widetilde{T}_\varepsilon$. Note that $a_{11} > a_{12}\widetilde{a}_{14}^*(\varepsilon) > a_{12}\widehat{a}_{14}^*(\varepsilon)$. Applying Lemma 2 (i) and comparison principle again, we have

$$\widetilde{x}^*(\varepsilon) \le \liminf_{t\longrightarrow+\infty} x(t) \le \limsup_{t\longrightarrow+\infty} x(t) \le \widehat{y}^*(\varepsilon), \tag{19}$$

where

$$\begin{aligned} \widetilde{x}^{**}(\varepsilon) &= \frac{-\left(\widetilde{a}_{14}^*(\varepsilon)a_{13} + a_{12}b_1\right) + \sqrt{\left(\widetilde{a}_{14}^*(\varepsilon)a_{13} + a_{12}b_1\right)^2 + 4b_1a_{13}\left(a_{11} - a_{12}\widetilde{a}_{14}^*(\varepsilon)\right)}}{2b_1a_{13}}, \\ \widehat{x}^{**}(\varepsilon) &= \frac{-\left(\widehat{a}_{14}^*(\varepsilon)a_{13} + a_{12}b_1\right) + \sqrt{\left(\widehat{a}_{14}^*(\varepsilon)a_{13} + a_{12}b_1\right)^2 + 4b_1a_{13}\left(a_{11} - a_{12}\widehat{a}_{14}^*(\varepsilon)\right)}}{2b_1a_{13}}. \end{aligned} \tag{20}$$

Letting $\varepsilon \longrightarrow 0^+$, we get $x^{**} \le \liminf_{t\longrightarrow+\infty} x(t) \le \limsup_{t\longrightarrow+\infty} x(t) \le x^{**}$ and hence $\lim_{t\longrightarrow+\infty} x(t) = x^{**}$. It follows that $\lim_{t\longrightarrow+\infty}(x(t), y(t)) = A_3$ and so A_3 is globally attractive in $(0,+\infty)\times(0,+\infty)$. This completes the proof. □

3. Numeric Simulations

In this section, we provide numeric simulations to illustrate the four situations in Theorem 3.

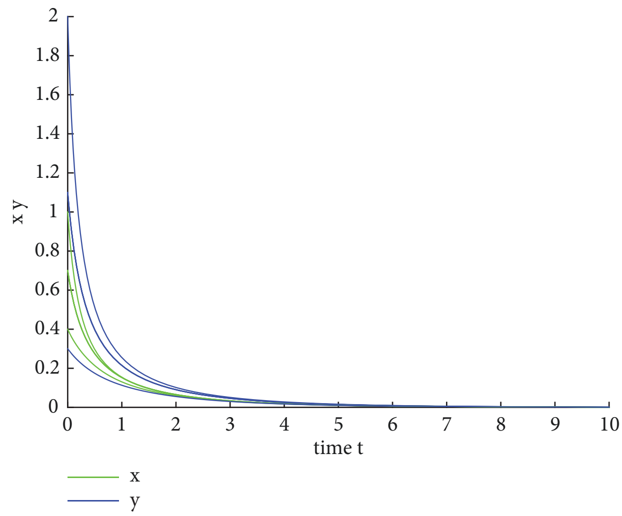

Figure 1: Solutions $(x(t), y(t))$ of system (21) with the initial conditions $(x(0), y(0)) = (1, 0.3)$, $(0.4, 2)$, and $(0.7, 1.1)$.

Example 4. Let $a_{11} = 3$, $a_{12} = 2$, $a_{13} = 2$, $a_{14} = 3$, $b_1 = 3$, $c_1 = 2$, $d_1 = 3$, $a_{21} = 1$, $a_{22} = 2$, $a_{23} = 3$, $a_{24} = 1$, and $b_2 = 2$. Then (5) becomes

$$\begin{aligned} \frac{dx}{dt} &= x\left(\frac{3}{2+2x} - 2 - 3x + \frac{2y}{3+y^2}\right), \\ \frac{dy}{dt} &= y\left(\frac{1}{2+3y} - 1 - 2y\right). \end{aligned} \tag{21}$$

Clearly, $a_{21} = 1 < 2 = a_{22}a_{24}$ and $a_{11} = 3 < 6 = a_{12}a_{14}$. By Theorem 3(i), the boundary equilibrium $A_0(0,0)$ is globally attractive. Figure 1 strongly supports it.

Example 5. Consider

$$\begin{aligned} \frac{dx}{dt} &= x\left(\frac{3}{1+x} - 2 - x + \frac{2y}{3+y^2}\right), \\ \frac{dy}{dt} &= y\left(\frac{4}{1+y} - 1 - y\right). \end{aligned} \tag{22}$$

Corresponding to (5), $a_{11} = 3, a_{12} = 1, a_{13} = 1, a_{14} = 2, b_1 = 1, c_1 = 2, d_1 = 3, a_{21} = 4, a_{22} = 1, a_{23} = 1, a_{24} = 1, b_2 = 1$. Obviously, $a_{11} > a_{12}a_{14} > a_{12}a_{14}^*$ and $a_{21} > a_{22}a_{24}$. It follows from Theorem 3 (iv) that $A_3 = (0.5, 1)$ is globally attractive (see Figure 2).

Example 6. Consider

$$\begin{aligned} \frac{dx}{dt} &= x\left(\frac{3}{1+x} - 2 - x + \frac{2y}{3+y^2}\right), \\ \frac{dy}{dt} &= y\left(\frac{1}{2+3y} - 1 - 2y\right); \end{aligned} \tag{23}$$

that is, we take $a_{11} = 3, a_{12} = 1, a_{13} = 1, a_{14} = 2, b_1 = 1, c_1 = 2, d_1 = 3, a_{21} = 1, a_{22} = 2, a_{23} = 3, a_{24} = 1, b_2 = 2$ in (5). This time, $a_{11} > a_{12}a_{14}$ and $a_{21} < a_{22}a_{24}$. Therefore, A_1 is globally attractive by Theorem 3 (ii), which is illustrated by Figure 3.

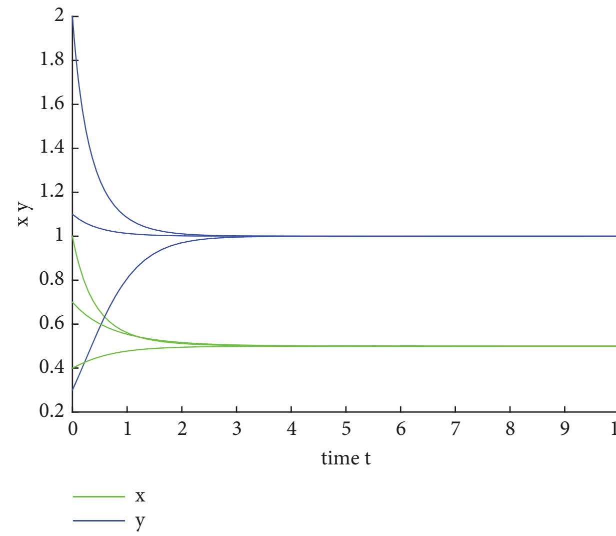

Figure 2: Solutions $(x(t), y(t))$ of system (22), with the initial conditions $(x(0), y(0)) = (1, 0.3)$, $(0.4, 2)$, and $(0.7, 1.1)$.

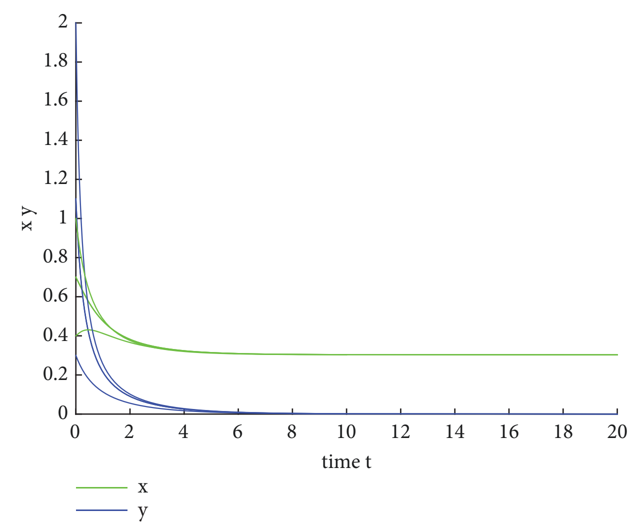

Figure 3: Solutions $(x(t), y(t))$ of system (23) with the initial conditions $(x(0), y(0)) = (1, 0.3)$, $(0.4, 2)$, and $(0.7, 1.1)$.

Example 7. Finally, let $a_{11} = 3, a_{12} = 2, a_{13} = 2, a_{14} = 3, b_1 = 3, c_1 = 2, d_1 = 3, a_{21} = 4, a_{22} = 1, a_{23} = 1, a_{24} = 1, b_2 = 1$ in (5); that is, consider

$$\begin{aligned} \frac{dx}{dt} &= x\left(\frac{3}{2+2x} - 2 - 3x + \frac{2y}{3+y^2}\right), \\ \frac{dy}{dt} &= y\left(\frac{4}{1+y} - 1 - y\right). \end{aligned} \tag{24}$$

Note that $a_{21} > a_{22}a_{24}$. We can calculate that $y^* = 1$ and $a_{14}^* = 5/2$. Then we see that $a_{11} = 3 < 5 = a_{12}a_{14}^*$. Thus it follows from Theorem 3 (iii) that A_2 is globally attractive (see Figure 4).

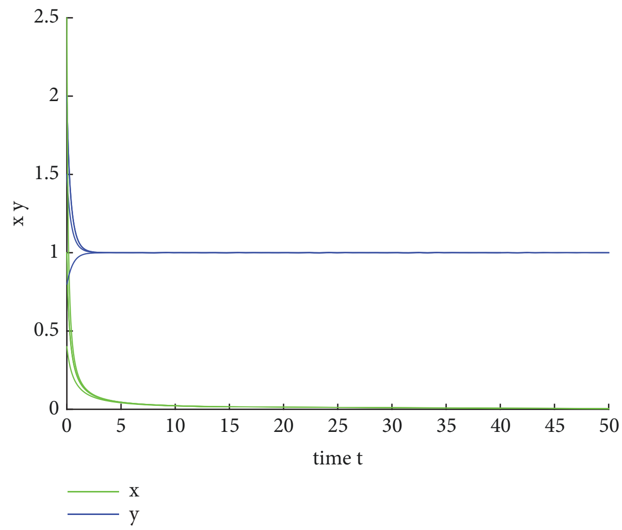

Figure 4: Solutions $(x(t), y(t))$ of system (24) with the initial conditions $(x(0), y(0)) = (1, 2), (0.4, 1.5)$, and $(2.5, 0.8)$.

4. Discussion

In this paper, inspired by the work in [17–19], we proposed a commensalism model under the assumption that the intrinsic growth rates of both species are density-dependent. The model can have at most four equilibria. For the first time, differential inequality has been applied to obtain the global attractivity of equilibria of such ecosystem models. Depending on the availability of resources, each of the possible equilibria can be globally attractive. This implies that density-dependent birth rates play an important role in the dynamics. Though the dynamics can be complicated, from the point view of commensalism, commensalism can be established only when resources for both species are large enough (see Theorem 3 (iv)). Hence, these results agree with those of Chen and Wu [5] (see Theorem A in Introduction).

As we know, delay always exists in many biological processes. We will leave the effect of delay on the dynamics for future study.

Data Availability

The data used to support the findings of this study are available from the corresponding author upon request.

Conflicts of Interest

The authors declare that there are no conflicts of interest.

Authors' Contributions

All authors contributed equally to the writing of this paper. All authors read and approved the final manuscript.

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