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ON THE ASYMMETRIC MAY–LEONARD MODEL OF THREE COMPETING SPECIES*

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Abstract. In this paper we analyze the global asymptotic behavior of the asymmetric May–Leonard model of three competing species: $\frac{dx_i}{dt} = x_i(1 - x_i - \beta_i x_{i-1} - \alpha_i x_{i+1})$, $x_i(0) > 0$, $i = 1, 2, 3$ with $x_0 = x_3$, $x_4 = x_1$ under the assumption $0 < \alpha_i < 1 < \beta_i$, $i = 1, 2, 3$. Let $A_i = 1 - \alpha_i$ and $B_i = \beta_i - 1$, $i = 1, 2, 3$. The linear stability analysis shows that the interior equilibrium $P = (p_1, p_2, p_3)$ is asymptotically stable if $A_1A_2A_3 > B_1B_2B_3$ and P is a saddle point with one-dimensional stable manifold Γ if $A_1A_2A_3 < B_1B_2B_3$. Hopf bifurcation occurs when $A_1A_2A_3 = B_1B_2B_3$. For the case $A_1A_2A_3 \neq B_1B_2B_3$ we eliminate the possibility of the existence of periodic solutions by applying the Stokes theorem. Then, from the Poincaré–Bendixson theorem for three-dimensional competitive systems, we show that (i) if $A_1A_2A_3 > B_1B_2B_3$ then P is global asymptotically stable in $\mathrm{Int}(\mathbf{R}^3_+)$, (ii) if $A_1A_2A_3 < B_1B_2B_3$ then for each initial condition $x_0 \notin \Gamma$, the solution $\varphi(t, x_0)$ cyclically oscillates around the boundary of the coordinate planes as the trajectory of the symmetric May–Leonard model does, and (iii) if $A_1A_2A_3 = B_1B_2B_3$ then there exists a family of neutrally stable periodic orbits.

Key words. asymmetric May–Leonard model, competition model of three species, Stokes theorem, Poincaré–Bendixson theorem for three-dimensional competitive systems, Butler–McGhee lemma, Hopf bifurcation

AMS subject classifications. 92D40, 34Cxx

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1. Introduction.

In this paper we analyze the global asymptotic behavior of the solutions of the following asymmetric May–Leonard model:

$$\begin{aligned} x_1' &= x_1(1 - x_1 - \alpha_1 x_2 - \beta_1 x_3), \\ x_2' &= x_2(1 - \beta_2 x_1 - x_2 - \alpha_2 x_3), \\ x_3' &= x_3(1 - \alpha_3 x_1 - \beta_3 x_2 - x_3), \\ & x_1(0) > 0,\ x_2(0) > 0,\ x_3(0) > 0, \end{aligned} \tag{1.1}$$

under the assumption

$$0 < \alpha_i < 1 < \beta_i, \qquad i = 1, 2, 3. \tag{1.2}$$

The Lotka–Volterra system (1.1) models the competition between three species with the same intrinsic growth rates and different competition coefficients. From the results of a two-dimensional competitive system [W], the assumption in (1.2) ensures that there is an orbit O_3 on the x_1x_2 plane connecting the equilibrium e_2 to the equilibrium e_1, an orbit O_2 on the x_1x_3 plane connecting the equilibrium e_1 to the equilibrium e_3, and an orbit O_1 on the x_2x_3 plane connecting equilibrium e_3 to the equilibrium e_2 where $e_1 = (1, 0, 0)$, $e_2 = (0, 1, 0)$, and $e_3 = (0, 0, 1)$. May and Leonard [ML] were the first to study the symmetric case of (1.1), i.e., $\alpha_i = \alpha$, $\beta_i = \beta$, $i = 1, 2, 3$. Under the assumptions $0 < \alpha < 1 < \beta$ and $\alpha + \beta > 2$, they showed that there exists a unique interior equilibrium $P = \frac{1}{1+\alpha+\beta}(1, 1, 1)$ which is a saddle point with

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one-dimensional stable manifold. They also found numerically that the system (1.1) exhibits a general class of solutions with nonperiodic oscillations of bounded amplitude but ever-increasing cycle time; asymptotically, "the system cycles from being composed almost wholly of population 1, to almost wholly 2, to almost wholly 3, back to almost wholly 1 etc." In [SSW] Schuster, Sigmund, and Wolf modified the proof in [ML] and rigorously showed that for each initial condition $x_0 = (x_1(0), x_2(0), x_3(0))$ in $\mathrm{Int}(\mathbf{R}^3_+)\backslash\Gamma$, the w limit set $w(x_0)$ of the solution $\varphi(t, x_0)$ of (1.1) is precisely the set $O_1 \cup O_2 \cup O_3$. Moreover, they studied the general asymmetric system (1.1) and showed that under the assumption (1.2) and the assumption

$$\beta_i - 1 > 1 - \alpha_j, \qquad 1 \le i,\ j \le 3, \tag{1.3}$$

there exists an open set of orbits in the interior of $\mathbf{R}^3_+$ having $O_1 \cup O_2 \cup O_3$ as w limit set.

In this paper we relax the assumption (1.3) to study the system (1.1). Under the basic assumption (1.2), we classify the global asymptotic behavior of the solutions of (1.1). In section 2 we shall show that under the assumption (1.2), the system (1.1) has a unique interior equilibrium $P = (p_1, p_2, p_3)$ and P is locally asymptotically stable provided $A_1A_2A_3 > B_1B_2B_3$, while P is a saddle point with one-dimensional stable manifold Γ provided $A_1A_2A_3 < B_1B_2B_3$ where the positive numbers $A_i = 1 - \alpha_i$ and $B_i = \beta_i - 1$, $i = 1, 2, 3$. In section 3, we prove the nonexistence of periodic solutions for the system (1.1) by Stokes theorem provided $A_1A_2A_3 \ne B_1B_2B_3$. In section 4, we employ the Poincaré-Bendixson theorem [H], [S] for three-dimensional competitive systems and the Butler–McGhee lemma [BW], [SW] to establish our main results. For the case $A_1A_2A_3 < B_1B_2B_3$, the equilibrium P is a saddle point with one-dimensional stable manifold Γ. We show that for $x_0 \notin \Gamma$, the w-limit set $w(x_0) = O_1 \cup O_2 \cup O_3$. Thus we generalize the results in [SSW]. For the case $A_1A_2A_3 > B_1B_2B_3$, the equilibrium P is locally asymptotically stable. We show that P is globally asymptotically stable with respect to the interior of $\mathbf{R}^3_+$. For the case $A_1A_2A_3 = B_1B_2B_3$, we show that the Hopf bifurcation occurs and there is a family of neutrally stable periodic solutions.

2. The local stability analysis. Under the assumption (1.2), the system (1.1) has the equilibria $O = (0, 0, 0)$, $e_1 = (1, 0, 0)$, $e_2 = (0, 1, 0)$, and $e_3 = (0, 0, 1)$ on the boundary of $\mathbf{R}^+_3$ and no other equilibria are on the coordinate planes. Obviously the equilibrium O is a repeller. From (1.2) it is easy to verify that the equilibrium e_1, e_2, e_3 attracts each point in the interior of the first quadrant of the x_1x_2, x_2x_3, x_1x_3 plane, respectively. Hence there is an orbit O_3 connecting the equilibrium e_2 to the equilibrium e_1, an orbit O_2 connecting the equilibrium e_1 to the equilibrium e_3, and an orbit O_1 connecting the equilibrium e_3 to the equilibrium e_2. Each e_i is a saddle point with two-dimensional stable manifold and one-dimensional unstable manifold. The orbits O_1, O_2, O_3 are the unstable manifolds of e_3, e_1, e_2, respectively.

In the following, we show that under the assumptions (1.2), the system (1.1) has a unique interior equilibrium P, and we perform the linear stability analysis of the equilibrium P.

LEMMA 2.1. *Let* (1.2) *hold. Then the system* (1.1) *has a unique interior equilibrium* $P = (p_1, p_2, p_3)$.

Proof. From (1.1), (p_1, p_2, p_3) satisfies the equations

$$\begin{aligned} x_1 + \alpha_1 x_2 + \beta_1 x_3 &= 1,\\ \beta_2 x_1 + x_2 + \alpha_2 x_3 &= 1,\\ \alpha_3 x_1 + \beta_3 x_2 + x_3 &= 1. \end{aligned} \tag{2.1}$$

Let

$$M = \begin{pmatrix} 1, & \alpha_1, & \beta_1 \\ \beta_2, & 1, & \alpha_2 \\ \alpha_3, & \beta_3, & 1 \end{pmatrix}, \quad \Delta = \det M, \quad \Delta_1 = \det \begin{pmatrix} 1, & \alpha_1, & \beta_1 \\ 1, & 1, & \alpha_2 \\ 1, & \beta_3, & 1 \end{pmatrix},$$

$$\Delta_2 = \det \begin{pmatrix} 1 & 1 & \beta_1 \\ \beta_2 & 1 & \alpha_2 \\ \alpha_3 & 1 & 1 \end{pmatrix}, \qquad \Delta_3 = \det \begin{pmatrix} 1 & \alpha_1 & 1 \\ \beta_2 & 1 & 1 \\ \alpha_3 & \beta_3 & 1 \end{pmatrix}.$$

From (1.2) we have

$$A_i = 1 - \alpha_i > 0, \quad B_i = \beta_i - 1 > 0, \quad i = 1, 2, 3. \tag{2.2}$$

A routine computation and (2.2) yield

$$\Delta_1 = A_1 A_2 + A_2 B_3 + B_3 B_1 > 0, \tag{2.3}$$

$$\Delta_2 = A_2 A_3 + A_3 B_1 + B_1 B_2 > 0, \tag{2.4}$$

$$\Delta_3 = A_3 A_1 + A_1 B_2 + B_2 B_3 > 0, \tag{2.5}$$

and

$$\begin{aligned} \Delta = {} & B_1 B_2 B_3 + B_1 B_2 + B_2 B_3 + B_3 B_1 + A_1 B_2 + A_2 B_3 + A_3 B_1 \\ & + A_1 A_2 + A_2 A_3 + A_3 A_1 (1 - A_2) > 0. \end{aligned} \tag{2.6}$$

Hence, from Cramer's rule it follows that

$$P = (p_1, p_2, p_3) = \left(\frac{\Delta_1}{\Delta}, \frac{\Delta_2}{\Delta}, \frac{\Delta_3}{\Delta} \right) > 0. \qquad \square \tag{2.7}$$

LEMMA 2.2. *The variational matrix of* (1.1) *at the equilibrium P, $DF(P)$ has -1 as its eigenvalue and P^t as an eigenvector associated with -1.*

Proof. A routine computation shows that the variational matrix of (1.1) at P is

$$\begin{aligned} DF(P) &= \begin{bmatrix} -p_1, & -\alpha_1 p_1, & -\beta_1 p_1 \\ -\beta_2 p_2, & -p_2, & -\alpha_2 p_2 \\ -\alpha_3 p_3, & -\beta_3 p_3 & -p_3 \end{bmatrix} \\ &= \begin{bmatrix} -p_1, & 0, & 0 \\ 0, & -p_2, & 0 \\ 0, & 0, & -p_3 \end{bmatrix} \begin{bmatrix} 1, & \alpha_1, & \beta_1 \\ \beta_2, & 1, & \alpha_2 \\ \alpha_3, & \beta_3, & 1 \end{bmatrix}. \end{aligned}$$

Then

$$DF(P) \begin{pmatrix} p_1 \\ p_2 \\ p_3 \end{pmatrix} = \begin{bmatrix} -p_1, & 0, & 0 \\ 0, & -p_2, & 0 \\ 0, & 0, & -p_3 \end{bmatrix} \begin{bmatrix} 1 \\ 1 \\ 1 \end{bmatrix} = - \begin{pmatrix} p_1 \\ p_2 \\ p_3 \end{pmatrix}.$$

Hence -1 is an eigenvalue of $DF(P)$ with associated eigenvector $(p_1, p_2, p_3)^t$. $\square$

We next compute the other two eigenvalues of $DF(P)$. Expand the characteristic polynomial of $DF(P)$,

$$\det(DF(P)-\lambda I) = \det\begin{pmatrix} -p_1-\lambda, & -\alpha_1 p_1, & -\beta_1 p_1 \\ -\beta_2 p_2, & -p_2-\lambda, & -\alpha_2 p_2 \\ -\alpha_3 p_3, & -\beta_3 p_3, & -p_3-\lambda \end{pmatrix}$$

$$= -\lambda^3 - \lambda^2(p_1+p_2+p_3) - \lambda(p_1p_2+p_2p_3+p_3p_1 - p_1p_2\alpha_1\beta_2 - p_2p_3\alpha_2\beta_3 \\ -p_3p_1\alpha_3\beta_1) - p_1p_2p_3 \det M.$$

Since -1 is an eigenvalue of $DF(P)$, we have

$$\det(DF(P)-\lambda I) = -(\lambda+1)\left[\lambda^2 + \lambda(p_1+p_2+p_3-1) + p_1p_2p_3\det M\right].$$

Then $\lambda_1 = -1$ and

$$\lambda_2, \lambda_3 = \frac{1}{2}\left[(1-p_1-p_2-p_3) \pm \sqrt{(p_1+p_2+p_3-1)^2 - 4p_1p_2p_3\det M}\right].$$

Claim:

$$(p_1+p_2+p_3-1)^2 - 4p_1p_2p_3\det M < 0.$$

Since

$$\Delta = \det M, \quad p_i = \frac{\Delta_i}{\Delta}, \quad i = 1,2,3,$$

from (2.3), (2.4), (2.5), (2.6), it follows that

$$\begin{aligned}
&(p_1+p_2+p_3-1)^2 - 4p_1p_2p_3\det M \\
&= \frac{1}{\Delta^2}\left[(\Delta_1+\Delta_2+\Delta_3-\Delta)^2 - 4\Delta_1\Delta_2\Delta_3\right] \\
&= \frac{1}{\Delta^2}\left[(B_1B_2B_3 - A_1A_2A_3)^2 - 4(A_1A_2+A_2B_3+B_3B_1)\right. \\
&\quad \left.(A_2A_3+A_3B_1+B_1B_2)(A_3A_1+A_1B_2+B_2B_3)\right] \\
&= \frac{1}{\Delta^2}\left[B_1^2B_2^2B_3^2 + A_1^2A_2^2A_3^2 - 2A_1A_2A_3B_1B_2B_3\right. \\
&\quad \left. -4\left(B_1^2B_2^2B_3^2 + A_1^2A_2^2A_3^2 + G(A_1,A_2,A_3,B_1,B_2,B_3)\right)\right] \\
&< 0,
\end{aligned}$$

where G is a homogeneous polynomial of A_i and B_j and $G > 0$. Hence the claim holds.

The real part of λ_2, λ_3 determines the local stability property of the equilibrium P. From (2.3)–(2.7), it is easy to verify that the real part of λ_2, λ_3 is

$$\frac{1}{2}(1-p_1-p_2-p_3) = \frac{1}{2\Delta}[\Delta-\Delta_1-\Delta_2-\Delta_3] = \frac{1}{2\Delta}\left[B_1B_2B_3 - A_1A_2A_3\right].$$

Hence it follows that P is locally asymptotically stable if $B_1B_2B_3 < A_1A_2A_3$ and P is a saddle point with one-dimensional stable manifold Γ if $B_1B_2B_3 > A_1A_2A_3$. The Hopf bifurcation occurs when $A_1A_2A_3 = B_1B_2B_3$.

3. Nonexistence of periodic solutions. In this section we prove that if $A_1A_2A_3 \neq B_1B_2B_3$, then the system (1.1) has no nontrivial periodic solutions.

Consider the system (1.1) with the assumptions (1.2),

$$\begin{aligned} \dot{x}_1 &= f_1(x_1,x_2,x_3) = x_1(1-x_1-\alpha_1 x_2-\beta_1 x_3),\\ \dot{x}_2 &= f_2(x_1,x_2,x_3) = x_2(1-\beta_2 x_1-x_2-\alpha_2 x_3),\\ \dot{x}_3 &= f_3(x_1,x_2,x_3) = x_3(1-\alpha_3 x_1-\beta_3 x_2-x_3),\\ & x_i(0)>0,\ i=1,2,3. \end{aligned} \tag{3.1}$$

Define a new vector field

$$(M_1,M_2,M_3) = (x_1,x_2,x_3)\times(f_1,f_2,f_3).$$

Then the routine computations yield

$$\begin{aligned} M_1 &= x_2x_3\left[(\beta_2-\alpha_3)x_1+(1-\beta_3)x_2+(\alpha_2-1)x_3\right],\\ M_2 &= x_1x_3\left[(\alpha_3-1)x_1+(\beta_3-\alpha_1)x_2+(1-\beta_1)x_3\right],\\ M_3 &= x_1x_2\left[(1-\beta_2)x_1+(\alpha_1-1)x_2+(\beta_1-\alpha_2)x_3\right], \end{aligned} \tag{3.2}$$

and

(3.3)
$$\begin{aligned} \operatorname{curl}(M_1,M_2,M_3) &= \left(\frac{\partial M_3}{\partial x_2}-\frac{\partial M_2}{\partial x_3},\frac{\partial M_1}{\partial x_3}-\frac{\partial M_3}{\partial x_1},\frac{\partial M_2}{\partial x_1}-\frac{\partial M_1}{\partial x_2}\right)\\ &= \begin{pmatrix} x_1\left[(A_3-B_2)x_1-(3A_1+B_3)x_2+(3B_1+A_2)x_3\right]\\ x_2\left[(3B_2+A_3)x_1+(A_1-B_3)x_2-(3A_2+B_1)x_3\right]\\ x_3\left[-(3A_3+B_2)x_1+(A_1+3B_3)x_2+(A_2-B_1)x_3\right] \end{pmatrix}. \end{aligned}$$

Let

$$\Gamma = \{(p_1t,p_2t,p_3t)|\ t>0\}. \tag{3.4}$$

LEMMA 3.1. *Γ is a positive invariant set under* (3.1), *and the solution $\psi(t)$ of* (3.1) *with initial condition in Γ satisfies*

$$\lim_{t\to\infty}\psi(t) = P.$$

Proof. If $x(0)\in\Gamma$ then $x(0)=(p_1\xi,p_2\xi,p_3\xi)$ for some $\xi>0$. Let $\phi(t)$ satisfy $\phi'(t)=\phi(t)(1-\phi(t)),\phi(0)=\xi$. Then it is easy to verify that $\psi(t)=(p_1\phi(t),p_2\phi(t),p_3\phi(t))$ satisfies (3.1). Hence Γ is positively invariant and $\lim_{t\to\infty}\psi(t)=P$. □

LEMMA 3.2. *Let $(x_1,x_2,x_3)\in R^3_+$ and $x_i>0$, $i=1,2,3$. If $(x_1,x_2,x_3)\notin\Gamma$ then $(M_1,M_2,M_3)\neq 0$ at (x_1,x_2,x_3).*

Proof. Since $(M_1,M_2,M_3)=(x_1,x_2,x_3)\times(f_1,f_2,f_3)$, if $(M_1,M_2,M_3)=0$, then either $(f_1,f_2,f_3)=0$ or $(f_1,f_2,f_3)=(x_1,x_2,x_3)t$ for some $t\in\mathbf{R}$. If $(f_1,f_2,f_3)=0$, then $(x_1,x_2,x_3)=P$. If $(f_1,f_2,f_3)=(x_1,x_2,x_3)t$, then

$$\begin{aligned} (1-x_1-\alpha_1x_2-\beta_1x_3) &= (1-\beta_2x_1-x_2-\alpha_2x_3)\\ &= (1-\alpha_3x_1-\beta_3x_2-x_3)=t. \end{aligned}$$

It follows that $(x_1,x_2,x_3)=(1-t)(p_1,p_2,p_3)\in\Gamma$.

Hence either of the above two cases leads to a contradiction to the assumption $(x_1, x_2, x_3) \notin \Gamma$. □

LEMMA 3.3. *The solutions of* (3.1) *are positive and bounded, and furthermore, for any* $\epsilon > 0$*, there exists* $T \geq 0$ *such that for each* $i = 1, 2, 3$*,* $x_i(t) < 1 + \epsilon$ *for all* $t \geq T$*.*

We omit the proof of Lemma 3.3 because it is quite standard.

THEOREM 3.4. *If* $A_1A_2A_3 \neq B_1B_2B_3$*, then the system* (3.1) *has no periodic solutions in the interior of* $\mathbf{R}^3_+$*.*

Proof. Suppose there exists a periodic solution $x(t) = (x_1(t), x_2(t), x_3(t))$, with period w, in the interior of $\mathbf{R}^3_+$. Let

$$C = \{(x_1(t), x_2(t), x_3(t)) |\ 0 \leq t \leq w\}.$$

We claim that the periodic orbit C is disjoint from the set Γ. From Lemma 3.1, it follows that if $C \cap \Gamma \neq \emptyset$, then $x(t) \to P$ as $t \to \infty$. This contradicts the fact that $x(t)$ is a periodic solution. Next, we construct the following conical surface S:

$$S = \{\lambda(x_1(t), x_2(t), x_3(t)) |\ \lambda \in [0, 1] \text{ and } t \in [0, w]\}.$$

Since (3.1) is a competitive system, from the nonordering principle, for any two points $x, y \in C$, $x \neq y$, x, y are unrelated; i.e., $x - y \notin \mathrm{Int}(\mathbf{R}^3_+)$ or $y - x \notin \mathrm{Int}(\mathbf{R}^3_+)$ (Proposition 3.3 in [S1]). Hence the surface S does not cross itself.

Given a point $(x_1(t_0), x_2(t_0), x_3(t_0)) \in C$, consider the segment from 0 to $x(t_0)$. Then from Lemma 3.2,

$$\begin{aligned} \vec{N} &= (x_1(t_0), x_2(t_0), x_3(t_0)) \times (f_1, f_2, f_3)|_{x=x(t_0)} \\ &= (M_1, M_2, M_3)|_{x=x(t_0)} \neq 0 \end{aligned}$$

is a normal vector of the surface S at each point of the segment $\overline{(0, x(t_0))}$.

Normalize the vector $\vec{N}$. Then we have the unit normal vector,

$$\vec{n} = \frac{1}{K_1}(M_1, M_2, M_3)|_{x=x(t_0)},$$

where $K_1 = |\vec{N}| \neq 0$. For each point on the segment $\overline{(0, x(t_0))}$, we compute $\mathrm{curl}(M_1, M_2, M_3) \cdot \vec{n}$ at the point $x = s(x_1(t_0), x_2(t)), x_3(t_0))$, $s \in [0, 1]$. Then from (3.3) and (3.2), it follows that

$$\begin{aligned} &\mathrm{curl}(M_1, M_2, M_3) \cdot \vec{n} \\ &= s^2 \mathrm{curl}(M_1, M_2, M_3)|_{x=x(t_0)} \cdot \frac{1}{K_1}(M_1, M_2, M_3)|_{x=x(t_0)} \\ &= s^2 \frac{1}{K_1} x_1x_2x_3\, G(x_1, x_2, x_3)|_{x=x(t_0)} \end{aligned}$$

where

$$\begin{aligned} &G(x_1, x_2, x_3) \\ &= (x_1, x_2, x_3) \left[\begin{pmatrix} B_2 + A_3 \\ -B_3 \\ -A_2 \end{pmatrix} (A_3 - B_2, 3A_1 - B_3, 3B_1 + A_2) \right. \end{aligned}$$

$$+\begin{pmatrix} -A_3 \\ B_3+A_1 \\ -B_1 \end{pmatrix}(3B_2+A_3, A_1-B_3, -3A_2-B_1)$$
$$\left. + \begin{pmatrix} -B_2 \\ -A_1 \\ B_1+A_2 \end{pmatrix}(-3A_3-B_2, 3B_3+A_1, A_2-B_1)\right] \begin{pmatrix} x_1 \\ x_2 \\ x_3 \end{pmatrix}.$$

A routine computation shows $G(x_1, x_2, x_3) = 0$.

Hence

$$\operatorname{curl}(M_1, M_2, M_3) \cdot \vec{n} = 0 \text{ on segment } \overline{(0, x(t_0))} \text{ for all } t_0 \in [0, w]$$

and

$$\operatorname{curl}(M_1, M_2, M_3) \cdot \vec{n} = 0 \quad \text{on the surface } S. \tag{3.5}$$

Let the surface $C' = \left\{(x_1, x_2, x_3) | \; x_1^{\delta_1} x_2^{\delta_2} x_3^{\delta_3} = c\right\}$ where the positive numbers $\delta_1, \delta_2, \delta_3$ will be selected and $c > 0$ is sufficiently small such that C' is disjoint from the periodic orbit C. Let Y be the intersection of the surface C' and the cone (bounded by S). Then C' divides the surface S into two parts S_1 and S_2 such that $C \subset S_1$ and $(0, 0, 0) \in S_2$.

Let $S' = Y \cup S_1$. Then S' is a surface with $\partial S' = C$. On the surface Y, the outward normal vector $\vec{N} = - \bigtriangledown (x_1^{\delta_1} x_2^{\delta_1} x_3^{\delta_3}) = -c(\frac{\delta_1}{x_1}, \frac{\delta_2}{x_2}, \frac{\delta_3}{x_3})$. Thus the outward unit normal vector $\vec{n}$ on Y is $\vec{n} = -\frac{c}{K_2}(\frac{\delta_1}{x_1}, \frac{\delta_2}{x_2}, \frac{\delta_3}{x_3})$ where $K_2 = |\vec{N}|$. From (3.3), it follows that on the surface Y, we have

$$\begin{aligned} \operatorname{curl}(M_1, M_2, M_3) \cdot \vec{n} = -\frac{c}{K_2} \{ & x_1((\delta_1+\delta_2-3\delta_3)A_3 - (\delta_1 - 3\delta_2 + \delta_3)B_2) \\ & + x_2(-(3\delta_1 - \delta_2 - \delta_3)A_1 - (\delta_1+\delta_2-3\delta_3)B_3) \\ & + x_3((\delta_1 - 3\delta_2+\delta_3)A_2 + (3\delta_1 - \delta_2 - \delta_3)B_1)\}. \end{aligned}$$

Choose $\delta_1, \delta_2, \delta_3$ satisfying

$$\begin{aligned} \delta_1 + \delta_2 - 3\delta_3 &= -A_1 B_2, \\ \delta_1 - 3\delta_2 + \delta_3 &= -A_1 A_3, \\ 3\delta_1 - \delta_2 - \delta_3 &= B_2 B_3 \end{aligned}$$

or

$$\begin{aligned} \delta_1 &= \frac{1}{4}(A_1B_2 + A_1A_3 + 2B_2B_3) > 0, \\ \delta_2 &= \frac{1}{4}(A_1B_2 + 2A_1A_3 + B_2B_3) > 0, \\ \delta_3 &= \frac{1}{4}(2A_1B_2 + B_2B_3 + A_1A_3) > 0. \end{aligned}$$

Then we have

$$\operatorname{curl}(M_1, M_2, M_3) \cdot \vec{n} = -\frac{c}{K_2} x_3(B_1B_2B_3 - A_1A_2A_3) < 0 \text{ or } > 0 \text{ for all } x \in Y. \tag{3.6}$$

Now we are in a position to prove Theorem 3.4 by Stokes's theorem [BD]. Since S_1 and Y are smooth enough for the application of Stokes's theorem,

$$\oint_C M_1 dx_1 + M_2 dx_2 + M_3 dx_3 = \int\int_{S_1 \cup Y} \operatorname{curl}(M_1, M_2, M_3) \cdot \vec{n} dA. \tag{3.7}$$

From the fact that $(M_1, M_2, M_3) = (x_1, x_2, x_3) \times (f_1, f_2, f_3)$, it follows that

$$\oint_C M_1 dx_1 + M_2 dx_2 + M_3 dx_3 = \int_0^w (M_1 f_1 + M_2 f_2 + M_3 f_3) dt = 0. \tag{3.8}$$

From (3.5) and (3.6)

$$\begin{aligned} &\int\int_{S_1 \cup Y} \operatorname{curl}(M_1, M_2, M_3) \cdot \vec{n} dA \\ &= \int\int_{S_1} \operatorname{curl}(M_1, M_2, M_3) \cdot \vec{n} dA + \int\int_Y \operatorname{curl}(M_1, M_2, M_3) \cdot \vec{n} dA \\ &= 0 - \frac{c}{K_2} \int\int_Y (B_1 B_2 B_3 - A_1 A_2 A_3) x_3 dA \neq 0. \end{aligned} \tag{3.9}$$

Thus (3.7), (3.8), (3.9) lead to a desired contradiction. □

THEOREM 3.5. *For the system* (1.1) *the periodic solutions exist if and only if* $A_1 A_2 A_3 = B_1 B_2 B_3$.

Proof. From Lemma 2.2, the variational matrix $DF(P)$ has eigenvalues $-1, \lambda_2, \lambda_3$ where

$$\lambda_2, \lambda_3 = \alpha(\mu) \pm i\beta(\mu),$$

$\alpha(\mu) = \mu \overset{\text{def}}{=} \frac{1}{2\Delta}[B_1 B_2 B_3 - A_1 A_2 A_3], \beta(\mu) > 0$. Obviously $\alpha(0) = 0, \alpha'(0) = 1$. By Hopf bifurcation [R, p. 226], there exists a periodic solution for $|\mu|$ sufficiently small. From Theorem 3.4, there exist no periodic solutions for $\mu \neq 0$, and thus we complete the proof of Theorem 3.5. □

Remark. From Theorem 3.4, the Hopf bifurcation for the system (1.1) is degenerate. In the next section we shall show that there is a family of neutrally stable periodic solutions for the case $A_1 A_2 A_3 = B_1 B_2 B_3$.

4. Global asymptotic behavior. In this section we analyze the global asymptotic behavior of the solutions of system (1.1) under the assumptions (1.2). In Theorem 4.3 we analyze the case $A_1 A_2 A_3 < B_1 B_2 B_3$ where the interior equilibrium P, from Lemma 3.1 and section 2, is a saddle point with one-dimensional stable manifold Γ, $\Gamma = \{(p_1 t, p_2 t, p_3 t) : t > 0\}$. In Theorem 4.4 we analyze the case $A_1 A_2 A_3 > B_1 B_2 B_3$ where the interior equilibrium P is locally asymptotically stable. In Theorem 4.5 we analyze the case $A_1 A_2 A_3 = B_1 B_2 B_3$ where Hopf bifurcation occurs. Before we prove these theorems we need the following lemma and theorem.

LEMMA 4.1 (Butler–McGhee [SW], [BW]). *Suppose that P is a hyperbolic equilibrium of an autonomous system $y' = f(y)$ which is in the ω-limit set, $w(x)$, of the positive orbit $\gamma^+(x)$ but is not the entire ω-limit set. Then $w(x)$ has a nontrivial (i.e., different from P) intersection with the stable and the unstable manifolds of P.*

The following is the Poincaré–Bendixson-like theorem for the competitive system in $\mathbf{R}^3$.

THEOREM 4.2 (see [H], [S], [S1]). *Let L be a compact α or w limit set of an irreducible cooperative or competitive system in $\mathbf{R}^3$. If L contains no equilibria then L is a closed orbit.*

THEOREM 4.3. *Let* (1.2) *hold and $A_1A_2A_3 < B_1B_2B_3$. For each $x_0 \in \mathrm{Int}(\mathbf{R}^3_+)\backslash\Gamma$, the ω-limit set $w(x_0)$ of the solution $\varphi(t, x_0)$ of* (1.1) *is precisely the set $O_1 \cup O_2 \cup O_3$.*

Proof. Since $x_0 \notin \Gamma$, $\lim_{t\to\infty} \varphi(t, x_0) \neq P$. From Theorems 3.4 and 4.2, it follows that $w(x_0)$ contains an equilibrium of the system (1.1). If $P \in w(x_0)$, then from the Butler–McGhee lemma there exists a point $y_0 \in \Gamma \cap w(x_0)$. From the invariance of the ω-limit set, we have either $\lim_{t\to-\infty} \varphi(t, y_0) = 0$ or $\lim_{t\to-\infty} \varphi(t, y_0) = \infty$. If $\lim_{t\to-\infty} \varphi(t, y_0) = 0$ then from the invariance of the ω-limit set, the origin O is in $w(x_0)$. This contradicts the fact that O is a repeller. From Lemma 3.3 the ω-limit set $w(x_0)$ is bounded. It is impossible that $\lim_{t\to-\infty} \varphi(t, y_0) = \infty$. Hence $P \notin w(x_0), O \notin w(x_0)$, and $e_i \in w(x_0)$ for some i. Without loss of generality, we assume that $e_1 \in w(x_0)$. Since e_1 is a saddle point with the x_1x_2 plane as its stable manifold and O_2 as its unstable manifold, we have $\lim_{t\to\infty} \varphi(t, x_0) \neq e_1$. Again from the Butler–McGhee lemma, there exists a point $y_0 \in O_2 \cap w(x_0)$. The invariance of ω-limit set yields $O_2 \subseteq w(x_0)$ and $e_3 \in w(x_0)$. The same arguments applied to e_3 yield that $O_1 \subseteq w(x_0)$, $e_2 \in w(x_0)$. Similarly $O_3 \subseteq w(x_0)$. Hence $O_1 \cup O_2 \cup O_3 \subseteq w(x_0)$.

Next we want to show that $w(x_0) \subseteq O_1 \cup O_2 \cup O_3$. First we show that $w(x_0) \cap \mathrm{bdry}(\mathbf{R}^3_+) \subseteq O_1 \cup O_2 \cup O_3$, where bdry $(\mathbf{R}^3_+)$ is the boundary of $\mathbf{R}^3_+$. If not, without loss of generality we may assume that there exist $y \in w(x_0)$ in the first quadrant of x_1x_2 plane, $y \notin O_3$. Then we have either $\lim_{t\to-\infty} \varphi(t, y) = O$ or $\lim_{t\to-\infty} \varphi(t, y) = \infty$. Both lead to a contradiction, as we argued before. To complete the proof of Theorem 4.3, it suffices to show that $w(x_0) \subseteq \mathrm{bdry}(\mathbf{R}^3_+)$.

Let $Q(x_1, x_2, x_3) = x_1^{\delta_1} x_2^{\delta_2} x_3^{\delta_3}$, where the positive numbers $\delta_1, \delta_2, \delta_3$ will be selected. Then we have

$$\frac{dQ}{dt} = QS \tag{4.1}$$

where

$$\begin{aligned} S(x_1, x_2, x_3) = (\delta_1 + \delta_2 + \delta_3)(1 - x_1 - x_2 - x_3) - x_1(\delta_2 B_2 - \delta_3 A_3) \\ - x_2(\delta_3 B_3 - \delta_1 A_1) - x_3(\delta_1 B_1 - \delta_2 A_2). \end{aligned} \tag{4.2}$$

From the assumption $B_1B_2B_3 > A_1A_2A_3$, we can choose $\delta_1, \delta_2, \delta_3 > 0$ satisfying

$$\begin{aligned} \delta_2 B_2 - \delta_3 A_3 > 0, \\ \delta_3 B_3 - \delta_1 A_1 > 0, \\ \delta_1 B_1 - \delta_2 A_2 > 0. \end{aligned} \tag{4.3}$$

Then $S(e_i) < 0$ for $i = 1, 2, 3$. Let $s > 0$ such that $S(e_i) < -s < 0$. Choose $r > 0$ such that $S(x) < -s$ on each open ball $N(e_i, r)$, $i = 1, 2, 3$. Set

$$\begin{aligned} \gamma_1 = O_1 \backslash \left(N(e_2, r) \cup N(e_3, r)\right), \\ \gamma_2 = O_2 \backslash \left(N(e_1, r) \cup N(e_3, r)\right), \\ \gamma_3 = O_3 \backslash \left(N(e_1, r) \cup N(e_2, r)\right), \end{aligned}$$

and

$$D = \left\{x \in \mathbf{R}^3_+ : \; S(x) < -s\right\}. \tag{4.4}$$

For each $x \in \gamma_i$, $i = 1, 2, 3$, there exists $T(x) \geq 0$ such that $\varphi(t, x) \in D$ for all $t \geq T(x)$. Let

$$m > \frac{2(\delta_1 + \delta_2 + \delta_3)}{s} + 1. \tag{4.5}$$

For each $x \in \cup_{i=1}^{3} \gamma_i$ from the property of continuous dependence on initial data, there exists $\delta(x) > 0$ such that $\varphi(t, y) \in D$ for all $y \in N(x, \delta(x))$ and $t \in [T(x), mT(x)+1]$. Since $\cup_{i=1}^{3} \gamma_i$ is a compact set and $\{N(x, \delta(x))\}_{x \in \gamma_i, i=1,2,3}$ covers $\cup_{i=1}^{3} \gamma_i$, there exists $x_1, \ldots, x_k \in \cup_{i=1}^{3} \gamma_i$ such that $\cup_{j=1}^{k} N(x_j, \delta(x_j)) \supseteq \cup_{i=1}^{3} \gamma_i$. Choose $\delta > 0$ sufficiently small such that the set

$$I(\delta) = \cup_{i=1}^{3} \left\{ y \in \mathbf{R}_+^3 : \operatorname{dist}(y, \gamma_i) < \delta \right\}$$

is contained in $\cup_{j=1}^{k} N(x_j, \delta(x_j))$. Let $T = \max_{1 \leq j \leq k} T(x_k)$.

To show that $w(x_0) \subseteq \operatorname{bdry}(\mathbf{R}_+^3)$, it suffices to show that $\lim_{t \to \infty} Q(\varphi(t, x_0)) = 0$. Set

$$\hat{q} = \inf \{ Q(x) : \ x \notin I(\delta) \text{ and } x \notin N(e_i, r) \text{ and } 0 \leq x_i \leq 1, i = 1, 2, 3 \}. \tag{4.6}$$

Choose $0 < \eta < \delta$ sufficiently small such that

$$\tilde{q} \exp\left((\delta_1 + \delta_2 + \delta_3) T \right) < \frac{\hat{q}}{2}, \tag{4.7}$$

where

$$\tilde{q} = \max \left\{ Q(x) : \ x \in \bar{I}(\eta) \right\}, \tag{4.8}$$

$$I(\eta) = \cup_{i=1}^{3} \left\{ y \in \mathbf{R}_+^3 : \ \operatorname{dist}(y, \gamma_i) < \eta \right\} \quad \text{and} \quad \bar{I}(\eta) \quad \text{is the closure of} \quad I(\eta).$$

Since $O_1 \cup O_2 \cup O_3 \subseteq w(x_0)$, there exists t_n sufficiently large such that $\varphi(t_n, x_0) \in I(\eta)$. Then

$$Q\left(\varphi(t_n, x_0) \right) < \tilde{q}. \tag{4.9}$$

Suppose $\varphi(t_n, x_0) \in N\left(x_j, \delta(x_j) \right)$ for some j. Then from (4.1), (4.2), (4.3), and (4.4), it follows that for $t_n \leq t \leq t_n + T(x_j)$

$$\begin{aligned} Q\left(\varphi(t, x_0) \right) &= Q\left(\varphi(t_n, x_0) \right) \exp\left(\int_{t_n}^{t} S(\varphi(t, x_0)) dt \right) \\ &\leq Q\left(\varphi(t_n, x_0) \right) \exp\left((\delta_1 + \delta_2 + \delta_3) T(x_j) \right) && (4.10) \\ &\leq Q\left(\varphi(t_n, x_0) \right) \exp\left((\delta_1 + \delta_2 + \delta_3) T \right) && (4.11) \end{aligned}$$

and

$$\begin{aligned} & Q\left(\varphi(t_n + mT(x_j) + 1, x_0) \right) \\ &= Q\left(\varphi(t_n + T(x_j), x_0) \right) \cdot \exp\left(\int_{t_n + T(x_j)}^{t_n + mT(x_j) + 1} S\left(\varphi(t, x_0) \right) dt \right) \\ &\leq Q\left(\varphi(t_n + T(x_j), x_0) \right) \exp\left(-s\left((m-1) T(x_j) + 1 \right) \right). && (4.12) \end{aligned}$$

From (4.10), (4.12), and (4.5), we have

$$
\begin{aligned}
&Q\left(\varphi(t_n + mT(x_j) + 1, x_0)\right)\\
&\le Q\left(\varphi(t_n, x_0)\right) e^{-s} \cdot \exp\left[(\delta_1 + \delta_2 + \delta_3 - s(m-1))\, T(x_j)\right]\\
&\le Q\left(\varphi(t_n, x_0)\right) e^{-s}. \qquad (4.13)
\end{aligned}
$$

From (4.9), (4.11), (4.7) it follows that for all $t \in [t_n, t_{n+}T(x_j)], \varphi(t, x_0)$ stays in either $I(\delta)$ or $U_{i=1}^3 N(x_i, r)$ and $Q(\varphi(t, x_0))$ is bounded by $Q(\varphi(t_n, x_0)) \exp((\delta_1 + \delta_2 + \delta_3)T)$. For $t \in [t_n + T(x_j), t_n + mT(x_j) + 1], \varphi(t, x_0)$ is decreasing and $Q(\varphi(t_n + mT(x_j) + 1, x_0)) \le Q(\varphi(t_n, x_0))e^{-s}$. Set $t_{n+1} = t_n + mT(x_j) + 1$; then $\varphi(t_{n+1}, x_0) \in I(\eta)$. Repeat the same arguments: we obtain a sequence $\{t_k\}_{k=n+1}^{\infty}, t_k \to \infty$, such that $Q(\varphi(t, x_0)) \le Q(\varphi(t_n, x_0))(e^{-s})^k \exp((\delta_1 + \delta_2 + \delta_3)T)$ for all $t \in [t_{n+k}, t_{n+k+1}]$. Hence it follows that $\lim_{t\to\infty} Q(\varphi(t, x_0)) = 0$. Thus we complete the proof of Theorem 4.3. □

THEOREM 4.4. *Let* (1.2) *hold and* $A_1A_2A_3 > B_1B_2B_3$. *Then the equilibrium* P *is globally asymptotically stable with respect to the interior of* $\mathbf{R}_+^3$.

Proof. Since $A_1A_2A_3 > B_1B_2B_3$, the equilibrium P is locally asymptotically stable. If P is not globally asymptotically stable with respect to the interior of $\mathbf{R}_+^3$, then the domain of attraction $W^+(P)$ of the equilibrium P is properly contained in $\text{Int}(\mathbf{R}_+^3)$. From Theorems 3.4 and 4.2, there exists no periodic orbit in $\text{Int}(\mathbf{R}_+^3)$ and there exists $x_0 \in \text{Int}(\mathbf{R}_+^3)\backslash W^+(P)$ such that the ω-limit set $w(x_0)$ contains an equilibrium. Similar arguments in Theorem 4.3 yield $O_1 \cup O_2 \cup O_2 \subseteq w(x_0)$. Introduce the function $Q(x_1, x_2, x_3) = x_1^{\delta_1} x_2^{\delta_2} x_3^{\delta_3}$ where the positive numbers $\delta_1, \delta_2, \delta_3$ will be selected. Then $Q(x)$ satisfies (4.1) and (4.2). From the assumption $A_1A_2A_3 > B_1B_2B_3$, we can choose $\delta_1, \delta_2, \delta_3 > 0$ satisfying

$$
\begin{aligned}
&\delta_2 B_2 - \delta_3 A_3 < 0,\\
&\delta_3 B_3 - \delta_1 A_1 < 0, \qquad (4.14)\\
&\delta_1 B_1 - \delta_2 A_2 < 0.
\end{aligned}
$$

Then $S(e_i) > 0$ for $i = 1, 2, 3$. Let $s > 0$ such that $S(e_i) > s$. Choose $r > 0$ such that $S(x) > s$ on each open ball $N(e_i, r)$, $i = 1, 2, 3$. Define the set $\gamma_1, \gamma_2, \gamma_3$ in (4.4) and

$$
D = \left\{x \in \mathbf{R}_+^3 : \; S(x) > s\right\}. \qquad (4.15)
$$

Following the same arguments in the proof of Theorem 4.3, we define $m, T(x)$, $\delta(x)$, x_k, $\delta(x_k)$, $\delta, I(\delta), T$ which have the same properties as in Theorem 4.3. Set

$$
\hat{q} = \inf\left\{Q(x) : \; x \notin I(\delta), x \notin N(e_i, r), 0 \le x_i \le 1, i = 1, 2, 3\right\}.
$$

Since $O_1 \cup O_2 \cup O_3 \subseteq w(x_0)$, there exists t_n sufficiently large such that $\varphi(t_n, x_0) \in I(\delta)$. Suppose $\varphi(t_n, x_0) \in N(x_j, \delta(x_j))$ for some j. Then from (4.1), (4.2), (4.14), (4.15) it follows that

$$
\begin{aligned}
&Q\left(\varphi(t_n + T(x_j), x_0)\right)\\
&= Q\left(\varphi(t_n, x_0)\right) \exp\left(\int_{t_n}^{t_n + T(x_j)} S(\varphi(t, x_0))dt\right)\\
&\ge Q(\varphi(t_n, x_0)) e^{-2(\delta_1 + \delta_2 + \delta_3)T(x_j)} \qquad (4.16)\\
&\ge Q(\varphi(t_n, x_0)) e^{-2(\delta_1 + \delta_2 + \delta_3)T}, \qquad (4.17)
\end{aligned}
$$

$$\begin{aligned} &Q\left(\varphi(t_n + mT(x_j) + 1, x_0)\right) \\ &= Q\left(\varphi(t_n + T(x_j), x_0)\right) \exp\left(\int_{t_n+T(x_j)}^{t_n+mT(x_j)+1} S\left(\varphi(t, x_0)\right) dt\right) \\ &\geq Q\left(\varphi(t_n + T(x_j), x_0)\right) \exp\left(s\left((m-1)T(x_j) + 1\right)\right). \end{aligned} \tag{4.18}$$

From (4.16), (4.18), and (4.5), we have

$$\begin{aligned} &Q\left(\varphi(t_n + mT(x_j) + 1, x_0)\right) \\ &\geq Q\left(\varphi(t_n, x_0)\right) e^s \exp\left(\left(-2(\delta_1 + \delta_2 + \delta_3) + s(m-1)\right) T(x_j)\right) \\ &\geq Q\left(\varphi(t_n, x_0)\right) e^s. \end{aligned} \tag{4.19}$$

Set $t_{n+1} = t_n + mT(x_j) + 1$. If $\varphi(t_{n+1}, x_0) \in I(\delta)$ then we repeat the same arguments to obtain $t_{n+2} > t_{n+1}$ satisfying $Q(\varphi(t_{n+2}, x_0)) > Q(\varphi(t_{n+1}, x_0))e^s > Q(\varphi(t_n, x_0))e^{2s}$. If we can continue this process, then there is a sequence $\{t_k\}_{k=n+1}^{\infty}$ such that $Q(\varphi(t_{n+k}, x_0)) > Q(\varphi(t_n, x_0))e^{ks}$. This leads to a contradiction that $Q(\varphi(t, x_0))$ is bounded for $t \geq 0$.

Thus it is impossible for the trajectory $\varphi(t, x_0)$ to stay in either $I(\delta)$ or $\cup_{i=1}^3 N(e_i, r)$ for all $t \geq t_n$. Hence there exists $\tau > 0$ such that $\varphi(t_n + \tau, x_0) \notin I(\delta)$ and $\varphi(t_n + \tau, x_0) \notin \cup_{i=1}^3 N(e_i, r)$. Then $Q(\varphi(t_n + \tau, x_0)) > \hat{q}$. From (4.17) and (4.19), $Q\left(\varphi(t, x_0)\right) \geq \hat{q}e^{-2(\delta_1+\delta_2+\delta_3)T}$ for all $t \geq t_n + \tau$. This contradicts the fact that $O_1 \cup O_2 \cup O_3 \subseteq w(x_0)$. Thus we complete the proof of Theorem 4.4. ◻

THEOREM 4.5. *Let* (1.2) *hold and* $A_1A_2A_3 = B_1B_2B_3$. *Then there exists a family of neutrally stable periodic orbits of* (1.1).

Proof. Let

$$\delta_1 = A_2B_3, \quad \delta_2 = B_1B_3, \quad \delta_3 = A_1A_2 \tag{4.20}$$

and surface

$$C = \left\{(x_1, x_2, x_3) \in \mathbf{R}_+^3 : \ x_1^{\delta_1} x_2^{\delta_2} x_3^{\delta_3} = 1\right\}. \tag{4.21}$$

Consider the plane π_k,

$$\frac{\delta_1}{p_1}x_1 + \frac{\delta_2}{p_2}x_2 + \frac{\delta_3}{p_3}x_3 = k, \tag{4.22}$$

where $k > 0$ is a parameter satisfying

$$\delta_1 + \delta_2 + \delta_3 \neq k\left(p_1^{\delta_1} p_2^{\delta_2} p_3^{\delta_3}\right). \tag{4.23}$$

When k is sufficiently large, the plane π_k intersects the surface C. Their intersection Γ_k is a closed curve. We construct the surface S_k by joining each point of Γ_k to the origin O. From (4.23) it follows that the equilibrium $P = (p_1, p_2, p_3)$ is not on the surface S_k. If the flow generated by (1.1) is invariant on the surface S_k, then from the fact that equilibrium O is a repeller and from Theorem 4.2, there exists at least a neutrally stable periodic orbit P_k on the surface S_k. Note that if $k_1 \neq k_2$, and both k_1 and k_2 satisfy (4.23), then $P_{k_1} \neq P_{k_2}$. It is easy to see that $\{P_k\}$ in fact forms a family of neutrally stable periodic orbits. Then we complete the proof of Theorem 4.5.

To show that the flow of (1.1) is invariant on S_k, it suffices to show that

$$\vec{F}\cdot\vec{N}=0 \quad \text{on} \quad S_k,$$

where $\vec{F}=(f_1,f_2,f_3)$ is the vector field of (1.1) and $\vec{N}$ is an outward normal vector on S_k. Let $(\hat{x}_1,\hat{x}_2,\hat{x}_3)\in\Gamma_k$ and

$$(x_1,x_2,x_3)=s\,(\hat{x}_1,\hat{x}_2,\hat{x}_3) \quad \text{for some } \ 0<s<1. \tag{4.24}$$

Let $\vec{T}$ be a tangent to the curve Γ_k at $(\hat{x}_1,\hat{x}_2,\hat{x}_3)$. Since $\Gamma_k=C\cap\pi_k$, then $\vec{T}$ is perpendicular to the normal vector of π_k, $(\frac{\delta_1}{p_1},\frac{\delta_2}{p_2},\frac{\delta_3}{p_3})$, and the normal vector of C, $\nabla(x_1^{\delta_1}x_2^{\delta_2}x_3^{\delta_3}|_{(x_1,x_2,x_3)=(\hat{x}_1,\hat{x}_2,\hat{x}_3)})$. Hence choose

$$\vec{T}=\left(\frac{\delta_1}{p_1},\frac{\delta_2}{p_2},\frac{\delta_3}{p_3}\right)\times\left(\frac{\delta_1}{\hat{x}_1},\frac{\delta_2}{\hat{x}_2},\frac{\delta_3}{\hat{x}_3}\right).$$

Then

$$\vec{T}=\left(\delta_2\delta_3\left(\frac{1}{p_2\hat{x}_3}-\frac{1}{p_3\hat{x}_2}\right),\delta_1\delta_3\left(\frac{1}{p_3\hat{x}_1}-\frac{1}{p_1\hat{x}_3}\right),\delta_1\delta_2\left(\frac{1}{p_1\hat{x}_2}-\frac{1}{p_2\hat{x}_1}\right)\right). \tag{4.25}$$

The normal vector $\vec{N}$ to the surface S_k at (x_1,x_2,x_3) is

$$\vec{N}=(\hat{x}_1,\hat{x}_2,\hat{x}_3)\times\vec{T}=(N_1,N_2,N_3).$$

Since $(\hat{x}_1,\hat{x}_2,\hat{x}_3)$ satisfies (4.22), then a routine computation shows

$$\begin{aligned} N_1&=\frac{\delta_1}{p_1}(\delta_1+\delta_2+\delta_3)-\frac{k}{\hat{x}_1}\delta_1,\\ N_2&=\frac{\delta_2}{p_2}(\delta_1+\delta_2+\delta_3)-\frac{k}{\hat{x}_2}\delta_2,\\ N_3&=\frac{\delta_3}{p_3}(\delta_1+\delta_2+\delta_3)-\frac{k}{\hat{x}_3}\delta_3. \end{aligned} \tag{4.26}$$

From (4.26), (4.24), and (3.1), a routine computation yields

$$\begin{aligned} \vec{F}\cdot\vec{N}=(\delta_1+\delta_2+\delta_3)&\left[\frac{\delta_1}{p_1}x_1+\frac{\delta_2}{p_2}x_2+\frac{\delta_3}{p_3}x_3-\frac{\delta_1}{p_1}\left(x_1^2+\alpha_1x_1x_2+\beta_1x_1x_3\right)\right.\\ &\left.-\frac{\delta_2}{p_2}\left(\beta_2x_1x_2+x_2^2+\alpha_2x_2x_3\right)-\frac{\delta_3}{p_3}\left(\alpha_3x_1x_3+\beta_3x_2x_3+x_3^2\right)\right]\\ &-\delta_1\left(\frac{\delta_1}{p_1}x_1+\frac{\delta_2}{p_2}x_2+\frac{\delta_3}{p_3}x_3\right)(1-x_1-\alpha_1x_2-\beta_1x_3)\\ &-\delta_2\left(\frac{\delta_1}{p_1}x_1+\frac{\delta_2}{p_2}x_2+\frac{\delta_3}{p_3}x_3\right)(1-\beta_2x_1-x_2-\alpha_2x_3)\\ &-\delta_3\left(\frac{\delta_1}{p_1}x_1+\frac{\delta_2}{p_2}x_2+\frac{\delta_3}{p_3}x_3\right)(1-\alpha_3x_1-\beta_3x_2-x_3). \end{aligned} \tag{4.27}$$

Canceling the term $(\delta_1+\delta_2+\delta_3)\left(\frac{\delta_1}{p_1}x_1+\frac{\delta_2}{p_2}x_2+\frac{\delta_3}{p_3}x_3\right)$ in (4.27) yields

$$\vec{F}\cdot\vec{N}=-x^{\top}Mx,$$

where

$$M = \begin{bmatrix} m_{11}, & m_{12}, & m_{13} \\ m_{21}, & m_{22}, & m_{23} \\ m_{31}, & m_{32}, & m_{33} \end{bmatrix}$$

with

$$\begin{aligned}
m_{11} &= \frac{\delta_1}{p_1}\left((\delta_1+\delta_2+\delta_3) - \delta_1 - \beta_2\delta_2 - \alpha_3\delta_3\right),\\
m_{22} &= \frac{\delta_2}{p_2}\left((\delta_1+\delta_2+\delta_3) - \alpha_1\delta_1 - \delta_2 - \beta_3\delta_3\right),\\
m_{33} &= \frac{\delta_3}{p_3}\left((\delta_1+\delta_2+\delta_3) - \beta_1\delta_1 - \alpha_2\delta_2 - \delta_3\right),\\
m_{12} &= \frac{\delta_1}{p_1}\left(\alpha_1(\delta_1+\delta_2+\delta_3) - \alpha_1\delta_1 - \delta_2 - \beta_3\delta_3\right),\\
m_{21} &= \frac{\delta_2}{p_2}\left(\beta_2(\delta_1+\delta_2+\delta_3) - \delta_1 - \beta_2\delta_2 - \alpha_3\delta_3\right),\\
m_{13} &= \frac{\delta_1}{p_1}\left(\beta_1(\delta_1+\delta_2+\delta_3) - \beta_1\delta_1 - \alpha_2\delta_2 - \delta_3\right),\\
m_{31} &= \frac{\delta_3}{p_3}\left(\alpha_3(\delta_1+\delta_2+\delta_3) - \delta_1 - \beta_2\delta_2 - \alpha_3\delta_3\right),\\
m_{23} &= \frac{\delta_2}{p_2}\left(\alpha_2(\delta_1+\delta_2+\delta_3) - \beta_1\delta_1 - \alpha_2\delta_2 - \delta_3\right),\\
m_{32} &= \frac{\delta_3}{p_3}\left(\beta_3(\delta_1+\delta_2+\delta_3) - \alpha_1\delta_1 - \delta_2 - \beta_3\delta_3\right).
\end{aligned} \tag{4.28}$$

From (4.28), (4.20) and the assumption $A_1A_2A_3 = B_1B_2B_3$, we have

$$\begin{aligned}
m_{11} &= \frac{\delta_1}{p_1}\left((1-\alpha_3)\delta_3 - (\beta_2-1)\delta_2\right) = 0,\\
m_{22} &= \frac{\delta_2}{p_2}\left((1-\alpha_1)\delta_1 - (\beta_3-1)\delta_3\right) = 0,\\
m_{33} &= \frac{\delta_3}{p_3}\left((1-\alpha_2)\delta_2 - (\beta_1-1)\delta_1\right) = 0.
\end{aligned} \tag{4.29}$$

From (2.7), (2.3), (2.4), (2.5), and $A_1A_2A_3 = B_1B_2B_3$, it follows that

$$p_1B_2 = p_3A_2, \quad p_2B_3 = p_1A_3, \quad p_3B_1 = p_2A_1. \tag{4.30}$$

From (4.32), (4.20), and (4.30) we have

$$\begin{aligned}
m_{12}+m_{21} &= \frac{\delta_1}{p_1}\left(-\delta_2A_1 - \delta_3(A_1+B_3)\right) + \frac{\delta_2}{p_2}\left(B\delta_2 + \delta_3(B_2+A_3)\right)\\
&= \frac{1}{p_1p_2}\left[\delta_2\left(A_1A_2A_3p_1 - A_2B_3A_1p_2\right) + \delta_1\left(B_1B_3B_2p_1 - A_1A_2B_3p_2\right)\right.\\
&\qquad \left. + \delta_3\left(B_1B_3B_2p_1 - A_2B_3A_1p_2\right)\right] = 0.
\end{aligned} \tag{4.31}$$

Similarly, we have

$$m_{13} + m_{31} = 0$$

and

$$m_{23} + m_{32} = 0. \tag{4.32}$$

Then (4.28), (4.31), (4.32) yield

$$\vec{F} \cdot \vec{N} = -x^\top M x = 0.$$

Thus we complete the proof of Theorem 4.5. □

5. Discussion. The general Lotka–Volterra system of three competing species can be scaled into the following form [Z]:

$$\begin{aligned} \frac{dx_1}{dt} &= r_1 x_1 \left(1 - x_1 - \alpha_1 x_2 - \beta_1 x_3\right), \\ \frac{dx_2}{dt} &= r_2 x_2 \left(1 - \beta_2 x_1 - x_2 - \alpha_2 x_3\right), \\ \frac{dx_3}{dt} &= r_3 x_3 \left(1 - \alpha_3 x_1 - \beta_3 x_2 - x_3\right), \\ &\alpha_i, \beta_i, r_i > 0, \quad i = 1, 2, 3. \end{aligned} \tag{5.1}$$

In this paper we study the case $r_1 = r_2 = r_3 = r$; i.e., the species have the same intrinsic growth rate. Let $\tau = rt$; then we convert the system (5.1) into (1.1). The assumption (1.2) states that only one species survives when the competition occurs among two species and species 1, 2, 3 are the winners of the competitions among species 1 and species 2, species 2 and species 3, species 3 and species 1, respectively. In [ML], May and Leonard showed that under the symmetric assumptions $\alpha_i = \alpha$, $\beta_i = \beta$, $i = 1, 2, 3$, the system (1.1) has nonperiodic oscillations if $\alpha + \beta > 2$. For the asymmetric case, Schuster, Sigmund, and Wolf [SSW] showed that if $\alpha_i + \beta_j > 2$, $j = 1, 2, 3$, there exists an open set of orbits of (1.1) having nonperiodic oscillations. Their result is local. In this paper we give a complete analysis for the global asymptotic behavior of the solutions of the asymmetric May–Leonard model (1.1). Under the assumptions (1.2), if $A_1A_2A_3 > B_1B_2B_3 \quad (A_i = 1 - \alpha_i, B_i = \beta_i - 1)$, then the populations will converge to a steady state. On the other hand, if $A_1A_2A_3 < B_1B_2B_3$, then the populations oscillate aperiodically around the coordinate planes. If $A_1A_2A_3 = B_1B_2B_3$, then Hopf bifurcation occurs and there is a family of neutrally stable periodic solutions.

Our results critically depend on the assumption $r_1 = r_2 = r_3 = r$ in (5.1). When r_1, r_2, r_3 are not identical, Zeeman [Z] shows that Hopf bifurcation may occur as parameters vary. Coste, Peyraud, and Coullet [CPC] perform the calculations to show that at the bifurcation point, a Hopf bifurcation is nondegenerate in the sense that it gives rise to a hyperbolic periodic orbit.

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