SIAM J. APPL. MATH.
Vol. 37, No. 1, August 1979

0036-1399/79/3701-0004 $01.00/0

ON ω-LIMITS FOR COMPETITION BETWEEN THREE SPECIES*

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Abstract. Following May and Leonard, we discuss some models of competition between three species. These models exhibit orbits converging to cycles which consist of three saddle points and three orbits connecting them.

1. Introduction. In [4] May and Leonard studied the equations

$$
\begin{aligned}
\dot{x}_1 &= x_1(1 - x_1 - \alpha x_2 - \beta x_3),\\
\dot{x}_2 &= x_2(1 - \beta x_1 - x_2 - \alpha x_3),\\
\dot{x}_3 &= x_3(1 - \alpha x_1 - \beta x_2 - x_3)
\end{aligned}
\tag{1}
$$

on the space $\mathbb{R}^3_+ = \{(x_1, x_2, x_3) \in \mathbb{R}^3 : x_i \geqq 0, i = 1, 2, 3\}$ with parameters $0 < \alpha < 1 < \beta$ and $\alpha + \beta > 2$. This is an equation of the Gauss–Lotka–Volterra type modeling competition between three species 1, 2, 3 whose densities are x_1, x_2, x_3. The four fixed points on the boundary of $\mathbb{R}^3_+$ (namely $(0, 0, 0)$, $e_1 = (1, 0, 0)$, $e_2 = (0, 1, 0)$ and $e_3 = (0, 0, 1)$) as well as the unique fixed point $C = (1 + \alpha + \beta)^{-1}(1, 1, 1)$ in the interior are unstable.

May and Leonard showed in their elegant study that such a system 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." [4]. The proof of this statement can be modified and supplemented, however, due to the fact that the orbits do not converge to the triangle formed by the intersections of the plane $x_1 + x_2 + x_3 = 1$ with the planes $x_1 = 0$, $x_2 = 0$ and $x_3 = 0$ respectively, i.e., to the boundary of the simplex S_3 spanned by e_1, e_2 and e_3.

In § 2 of this note we give such a modified discussion of (1) and describe the ω-limit sets. In § 3 we show that even if the symmetry condition of (1) is dropped, there are orbits with the same cyclic asymptotic behavior. In § 4, finally, we give an example of an ecological equation whose orbits have the ω-limit described in [4], namely the boundary of the simplex S_3.

2. The model of May and Leonard [4]. Consider first the restriction of (1) to the plane $x_3 = 0$. In the positive quadrant, $\dot{x}_1 = 0$ on the segment joining $(0, 1/\alpha)$ to $(1, 0)$ and $\dot{x}_2 = 0$ on the segment between $(0, 1)$ and $(1/\beta, 0)$. These segments are disjoint. There are three fixed points, namely: $(0, 0)$, which is a source having 1 as double eigenvalue; $(1, 0)$ which is a sink, with eigenvalues -1 and $1 - \beta$; and $(0, 1)$ which is a saddle, the eigenvalues being -1 and $1 - \alpha$. (A phase portrait is sketched in Fig. 1.) Note the unstable manifold of $(0, 1)$, (a separatrix), which is an orbit o_3 with α-limit $(0, 1)$ and ω-limit $(1, 0)$. (The segment between $(0, 1)$ and $(1, 0)$ is not invariant, incidentally.)

Returning to $\mathbb{R}^3_+$, we see that there is an orbit o_3 in the plane $x_3 = 0$ from e_2 to e_1, an orbit o_2 in the plane $x_2 = 0$ from e_1 to e_3 and an orbit o_1 in the plane $x_1 = 0$ from e_3 to e_2. Let F denote the union of the three orbit closures (see Fig. 2).

THEOREM 1. *With the exception of the fixed point C, every orbit in the interior of $\mathbb{R}^3_+$ has F as ω-limit.*

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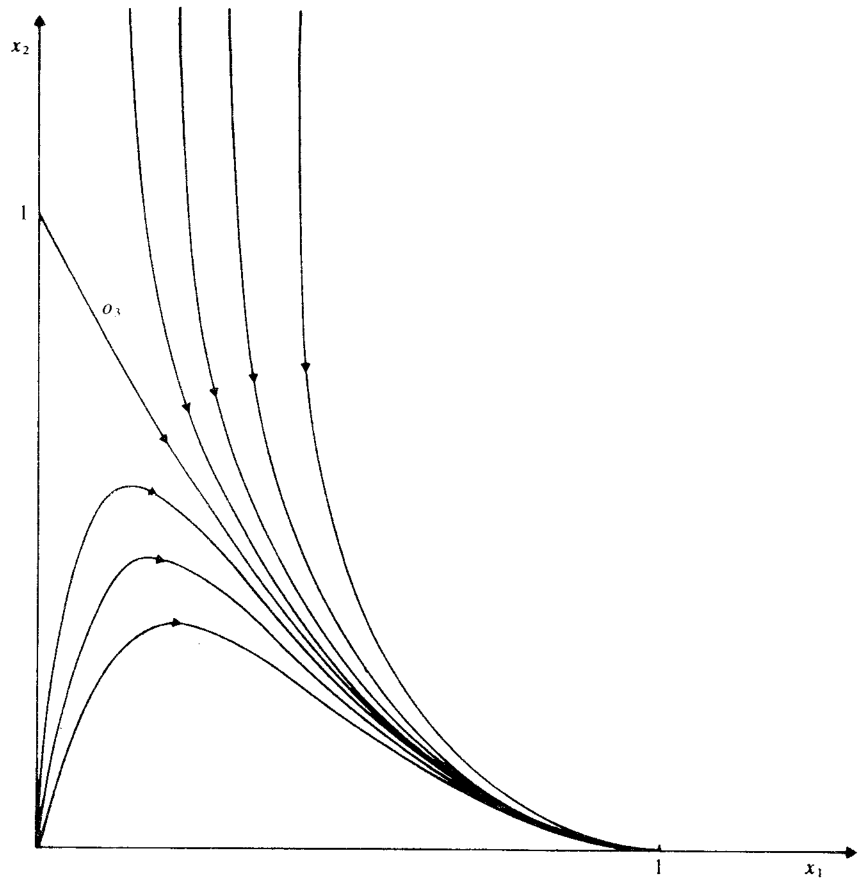

FIG. 1. *Computer graph of orbits of* (1) *in the plane* $x_3 = 0$.

Proof. If $V = x_1 + x_2 + x_3$, then

$$\dot{V} = x_1 + x_2 + x_3 - [x_1^2 + x_2^2 + x_3^2 + (\alpha + \beta)(x_1x_2 + x_2x_3 + x_3x_1)]$$
$$= V - (x_1, x_2, x_3)^T A(x_1, x_2, x_3)$$

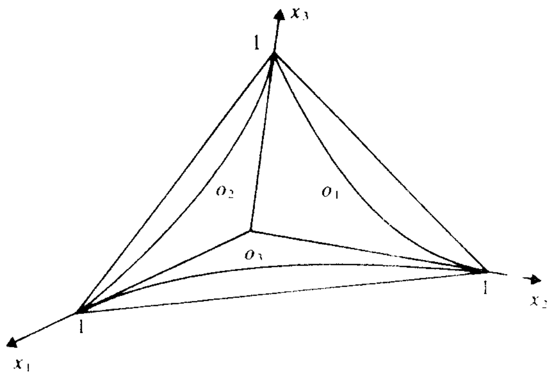

FIG. 2. *The union of* o_1, o_2 *and* o_3 *is the* ω*-limit of almost every orbit of* (1).

where A is the matrix

$$\begin{bmatrix} 1 & \frac{\alpha+\beta}{2} & \frac{\alpha+\beta}{2} \\ \frac{\alpha+\beta}{2} & 1 & \frac{\alpha+\beta}{2} \\ \frac{\alpha+\beta}{2} & \frac{\alpha+\beta}{2} & 1 \end{bmatrix}$$

which is symmetric and circulant and has the eigenvalues

$$\lambda_1 = 1+\alpha+\beta > 0,$$

$$\lambda_{2,3} = 1-(\alpha+\beta) < 0.$$

Thus the quadric

$$V-(x_1, x_2, x_3)^T A(x_1, x_2, x_3) = 0$$

is a two-sheeted hyperboloid with center $(1+\alpha+\beta)^{-1}(\frac{1}{2}, \frac{1}{2}, \frac{1}{2})$ and rotational symmetry around the axis $x_1 = x_2 = x_3$. The origin and the equilibrium point C lie on this axis and on the quadric. The sheet through $(0, 0, 0)$ contains no other point of $\mathbb{R}^3_+$. The sheet through C (see Fig. 3) contains also e_1, e_2 and e_3 and for every point (x_1, x_2, x_3) on this sheet one has $V \geqq 3/(1+\alpha+\beta)$ with equality iff $(x_1, x_2, x_3) = C$. If, furthermore, $(x_1, x_2, x_3) \in \mathbb{R}^3_+$, then $V \leqq 1$ with equality iff (x_1, x_2, x_3) is one of the o_i.

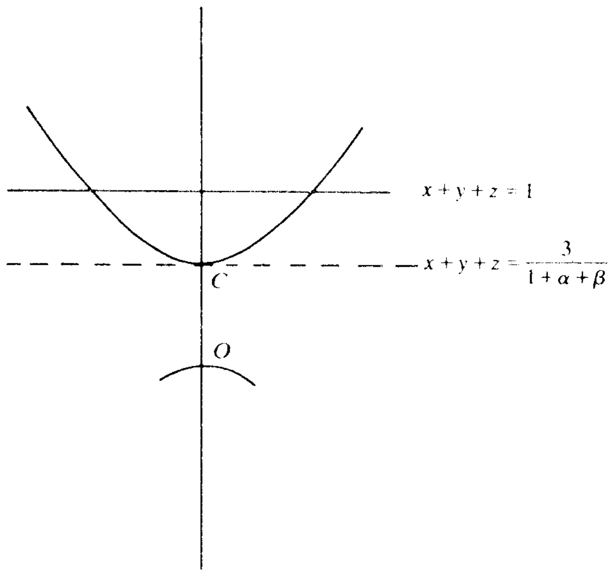

FIG. 3. *Intersection of the hyperboloid with a plane through the symmetry axis.*

The points in the interior of $\mathbb{R}^3_+$ satisfying $\dot{V} = 0$ are just those on the sheet; hence every orbit in the interior of $\mathbb{R}^3_+$ enters the set

$$Q_1 = \{(x_1, x_2, x_3) \in \mathbb{R}^3_+ : 3/(1+\alpha+\beta) < V \leqq 1\}$$

and remains inside (with the exception of the fixed point C and one orbit whose ω-limit is C).

With $P = x_1x_2x_3$ one has

$$\dot{P} = P(3-(1+\alpha+\beta)V).$$

In $\bar{Q}_1$, P has a local extremum in C. With the exception of one orbit whose ω-limit is C, all other orbits in Q_1 approach the set where $P=0$, i.e., the boundary of $\mathbb{R}^3_+$. This shows that the orbits of almost all points in $\mathbb{R}^3_+$ approach the set $Q_1 \cap bd\mathbb{R}^3_+$ and hence have their ω-limits in this set. Such an ω-limit W has to be invariant and, by [1], T_1-connected. This means that for any $\varepsilon > 0$ and and $x, y \in W$, there is a chain $z_0 = x, z_1, \cdots, z_n = y$ in W with $d(T_1 z_i, z_{i+1}) < \varepsilon$ for $i = 0, \cdots, n-1$. (d is Euclidean metric and T_t denotes the one parameter group of transformations defined by (1).) The fixed points e_1, e_2 and e_3 cannot be ω-limits of orbits in the interior of $\mathbb{R}^3_+$ since they are saddles. The only remaining invariant T_1-connected set in $Q_1 \cap bd\mathbb{R}^3_+$ is F, which therefore must be the ω-limit.

3. A generalized, unsymmetric model. In [4] May and Leonard state that it is plausible that qualitative features of (1) will remain true in the more general unsymmetric case. Here we consider the equations

$$\begin{aligned} \dot{x}_1 &= x_1(1-x_1-\alpha x_2-\beta_1 x_3), \\ \dot{x}_2 &= x_2(1-\beta_2 x_1-x_2-\alpha_2 x_3), \qquad (2) \\ \dot{x}_3 &= x_3(1-\alpha_3 x_1-\beta_3 x_2-x_3), \end{aligned}$$

with $0 < \alpha_i < 1 < \beta_i$ and $\beta_i - 1 > 1 - \alpha_j$ $(1 \leqq i, j \leqq 3)$ and show that they have indeed cycles of ever lengthening period just as in the symmetric case. Note first that the fixed points on the boundary of $\mathbb{R}^3_+$ and the phase portrait are just as for (1) (but of course the orbits o_1, o_2 and o_3 are no longer congruent). Defining F as before, we shall prove

THEOREM 2. *There exists an open set of orbits in the interior of $\mathbb{R}^3_+$ having F as ω-limit.*

Proof. With $V = x_1+x_2+x_3$ one has

$$\dot{V} = V - [x_1^2+x_2^2+x_3^2+(\alpha_1+\beta_2)x_1x_2+(\alpha_2+\beta_3)x_2x_3+(\alpha_3+\beta_1)x_3x_1] \leqq V(1-V)$$

(because $\alpha_1+\beta_2>2$ etc. $\cdots$); hence all orbits enter the set

$$Q_2 = \{(x_1, x_2, x_3) \in \mathbb{R}^3_+ : r < x_1+x_2+x_3 < 1+r\}$$

with some $r>0$ small enough.

Set $s_1 = 1+\beta_2+\alpha_3$, $s_2 = 1+\beta_3+\alpha_1$, $s_3 = 1+\beta_1+\alpha_2$ and $S = 3 - s_1x_1 - s_2x_2 - s_3x_3$. With $P = x_1x_2x_3$ one has $\dot{P} = PS$. Since $s_i > 3$ for $i = 1, 2, 3$, one has $S(e_i) < 0$. Choose $s > 0$ such that $S(e_i) < -s$ and let

$$B = \{(x_1, x_2, x_3) \in Q_2 : S(x_1, x_2, x_3) < -s\}.$$

Since every $x \in Q_2 \cap bd\mathbb{R}^3_+$ has e_1, e_2 or e_3 as ω-limit, we may define

$$T(x) = \inf\{T' \geqq 0 : x(t) \in B \text{ for } T' \leqq t \leqq (m+1)T'+1\} \qquad (3)$$

where $m > 3/s$. For such x there is a $T' < T(x)+1$ with $x(t) \in B$ for $T' \leqq t \leqq (m+1)T'+1$. Thus on the set

$$I = \{y \in Q_2 : d(x, y) < \delta(x) \text{ for some } x \in Q_2 \cap bd\mathbb{R}^3_+\}$$

one can define T just as in (3). T is upper semicontinuous on I, and hence admits an upper bound L. Now choose $\delta > 0$ so small that

$$\bar{I}(\delta) \doteq \{y \in Q_2 : d(y, bd\mathbb{R}^3_+) \leqq \delta\}$$

is contained in I, and let

$$p=\inf\{P(y): y\in Q_2\setminus\bar{I}(\delta)\}.$$

Choose $\varepsilon>0$ so small that with

$$I(\varepsilon)\doteq\{y\in Q_2: 0<d(y, bd\mathbb{R}^3_+)<\varepsilon\}$$

and

$$p'=\sup\{P(x): x\in I(\varepsilon)\}$$

one has

$$p'\exp(3L)<p.$$

We claim now that the orbit of every $x\in I(\varepsilon)$ has F as ω-limit. For this, it suffices to check that $P(x(t))\to 0$, for $t\to+\infty$. Indeed, while there might be time-intervals $[t_1, t_2]$ during which $P(x(t))$ increases, their length L' must be smaller than L, and hence

$$P(x(t_2))\leqq P(x(t_1))\exp(3L').$$

At the end of such an interval, the orbit enters B and stays there for a time at least equal to $mL'+1$. So for $t_3=t_2+mL'+1$ one has

$$P(x(t_3))\leqq P(x(t_2))\exp(-s(mL'+1))$$
$$\leqq P(x(t_1))\exp(-s).$$

Thus $P(x(t))$ can never grow too much (in particular, $x(t)$ can never leave $\bar{I}(\delta)$) and every period of growth is subsequently compensated, so that $P(x(t))\to 0$. The rest of the proof is similar to that of Theorem 1.

4. A related model with constraints of "constant organization" [2]. We now briefly discuss a class of equations reflecting cyclic competition whose phase portrait looks just like the one described in [4]. These equations belong to the class of equations with constant organization which is studied as a model for the selforganization of macromolecules (see [2], [3], and [5]).

Consider in $\mathbb{R}^3_+$ the equations

$$\begin{aligned}\dot{x}_1&=x_1(x_1+\alpha x_2+\beta x_3-M),\\ \dot{x}_2&=x_2(\beta x_1+x_2+\alpha x_3-M),\\ \dot{x}_3&=x_3(\alpha x_1+\beta x_2+x_3-M),\end{aligned}\tag{4}$$

where $M=x_1(x_1+\alpha x_2+\beta x_3)+x_2(\beta x_1+x_2+\alpha x_3)+x_3(\alpha x_1+\beta x_2+x_3)$. We shall consider the case $0<\alpha<1<\beta$, $\alpha+\beta<2$. Apart from the origin (which is a source) there are three fixed points on the boundary of $\mathbb{R}^3_+$, namely e_1, e_2 and e_3. They are saddle points with eigenvalues -1, $\beta-1>0$, $\alpha-1<0$. There is just one more fixed point in $\mathbb{R}^3_+$, namely $C=(\frac{1}{3},\frac{1}{3},\frac{1}{3})$ with eigenvalues -1 and $\frac{1}{6}(2-\alpha-\beta\pm i\sqrt{3}(\beta-\alpha))$, which is a saddle point. (Three more fixed points of (4) lie outside $\mathbb{R}^3_+$).

With $V=x_1+x_2+x_3$ one has

$$\dot{V}=M(1-V)$$

and so every orbit in $\mathbb{R}^3_+$ (with the exception of the origin) converges to the invariant simplex

$$S_3=\{(x_1,x_2,x_3)\in R^3_+: x_1+x_2+x_3=1\}.$$

With $P = x_1x_2x_3$ one has

$$\dot{P} = P[(1+\alpha+\beta)V - 3M]$$
$$= P[(1+\alpha+\beta)(x_1+x_2+x_3) - 3(x_1^2+x_2^2+x_3^2+(\alpha+\beta)(x_1x_2+x_2x_3+x_3x_1))]$$
$$= P[(1+\alpha+\beta)(1-V)\;V+\tfrac{1}{2}(\alpha+\beta-2)((x_1-x_2)^2+(x_2-x_3)^2+(x_3-x_1)^2)].$$

On S_3 one has $V=1$, and $\alpha+\beta<2$ implies that $\dot{P}\leqq 0$, with equality iff (x_1, x_2, x_3) is C or lies on the boundary. Hence we obtain

THEOREM 3. *The orbit of almost every point in the interior of $\mathbb{R}^3_+$ has as ω-limit the boundary of S_3, formed by the points e_1, e_2, e_3 and the three segments (which are orbits) joining them.*

(The exceptional points are C and its stable manifold, which consists of the two orbits on the line $x_1 = x_2 = x_3$ having C as ω-limit.) See Fig. 4 for a sketch of the phase portrait.

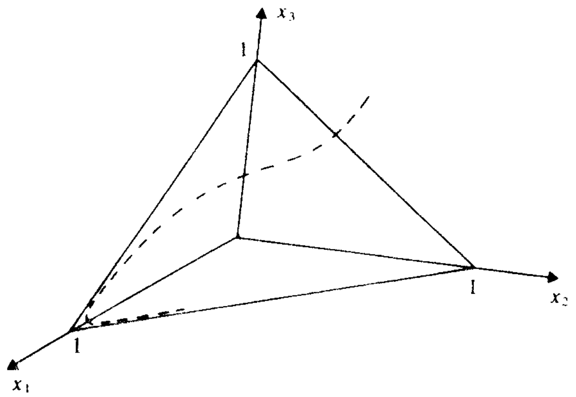

FIG. 4. *The boundary of the simplex is the ω-limit of almost every orbit of* (4).

In the limiting case $\alpha+\beta=2$ for (1), which was studied in [4, § 3], S_3 consists of closed orbits defined by $x_1x_2x_3 = \text{const.}$, and every orbit in the interior of $\mathbb{R}^3_+$ has one of these closed orbits as ω-limit.

For a more general discussion and comparison with related dynamical systems we refer to [5].

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