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Stable Periodic Solutions for the Hypercycle System

J. Hofbauer,[1] J. Mallet-Paret,[2] and H. L. Smith[3]

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We consider the hypercycle system of ODEs, which models the concentration of a set of polynucleotides in a flow reactor. Under general conditions, we prove the omega-limit set of any orbit is either an equilibrium or a periodic orbit. The existence of an orbitally asymptotic stable periodic orbit is shown for a broad class of such systems.

KEY WORDS: Competitive systems; cyclic systems; hypercycle system; monotonicity; Poincaré–Bendixson.

0. INTRODUCTION

The hypercycle system of differential equations is a simple model of the time evolution of the concentrations of a set of polynucleotides, M_1, $M_2,\dots, M_n$, in a flow reactor in which M_1 catalyzes the replication of M_2, M_2 that of M_3, and so on, finally, M_n catalyzes the replication of M_1. The hypercycle was proposed by Eigen [1] to show that cooperation can lead to coexistence of these information carrying macromolecules. The dynamical form of this coexistence is the subject of the present work. As a corollary of our main result, we answer in the affirmative the conjecture of Schuster *et al.* [10] that there exists a stable periodic solution for long (large n) hypercycles.

This paper is heavily dependent upon the results and proofs in [8]. We do not reproduce in their entirety arguments which are substantially similar to those already presented in this reference. We always, however, give detailed references for these arguments.

[1] Institut für Mathematik, Universität Wien, A-1090 Wien, Austria.
[2] Division of Applied Mathematics, Brown University, Providence, Rhode Island 02912.
[3] Department of Mathematics, Arizona State University, Tempe, Arizona 85257.

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We consider the dynamical system described by the following system of differential equations:

$$\dot{x}_i = x_i \left[F_i(x_i, x_{i-1}) - \sum x_j F_j(x_j, x_{j-1}) \right] \tag{0.1}$$

where $1 \leqslant i \leqslant n$ and we agree to interpret i modulo n. The F_i are continuously differentiable functions further described below. The system (0.1) defines a dynamical system on S_{n-1}, the standard $n-1$ simplex in $\mathbb{R}^n_+$, given by

$$S_{n-1} = \left\{ x \in \mathbb{R}^n_+ : \sum x_i = 1 \right\}$$

$\mathbb{R}^n_+$ is the usual cone of nonnegative vectors in $\mathbb{R}^n$, Int $\mathbb{R}^n_+$ denotes the interior of $\mathbb{R}^n_+$, and $S^*_{n-1} = S_{n-1} \cap \text{Int}\, \mathbb{R}^n_+$. By a solution of (0.1) on S_{n-1}, we always mean a solution defined on $[0, \infty)$.

Our main assumptions are now described.

(H1) (0.1) is *permanent* on S_{n-1}. That is, there exists a positive number ρ such that every solution, $x(t)$, with $x(0) \in S^*_{n-1}$ satisfies $x_i(t) > \rho$ for each i and for all large values of t.

(H2) $F_i(x_i, x_{i-1})$ are continuously differentiable functions defined for nonnegative values of their arguments and satisfying

$$\frac{\partial F_i}{\partial x_{i-1}} > 0 \tag{0.2}$$

for every i.

(H3) S^*_{n-1} contains a unique equilibrium point p of (0.1). Furthermore,

$$\text{Det}\, DF(p) \neq 0 \tag{0.3}$$

(H4) $F = (F_1, F_2, ..., F_n)$ is homogeneous of degree $q > 0$:

$$F(sx) = s^q F(x), \qquad s \geqslant 0, \qquad x \in \mathbb{R}^n_+ \tag{0.4}$$

A special class of systems of the above type which have received considerable attention in the literature is given by

$$F_i = a_i x_i + b_{i-1} x_{i-1}, \qquad a_i \geqslant 0, \qquad b_i > 0 \tag{0.5}$$

Sufficient conditions for (0.1) with (0.5) to be permanent are known. If $a_i = 0$ for all i, then (0.1) is permanent; if $a_i > 0$ for all i, then (0.1) is permanent if and only if the matrix

$$\begin{matrix} d_1 & -1 & -1 & \cdots & -1 & 0 \\ 0 & d_2 & -1 & \cdots & -1 & -1 \\ -1 & 0 & d_3 & \cdots & -1 & -1 \\ \cdot & \cdot & \cdot & & \cdot & \cdot \\ -1 & -1 & -1 & \cdots & 0 & d_n \end{matrix} \tag{0.6}$$

is an M-matrix, where $d_i = (b_i/a_i) - 1$. See Ref. 7 (p. 189). Recall that a square matrix is an M matrix if its off-diagonal entries are nonpositive and if all principal minors are positive. If F is given by (0.5), then (H1)–(H4) are not independent of each other. In Ref. 7 it is shown that (H1) implies (H3), including (0.3), when F is given by (0.5). Obviously in this case (H2) and (H4) hold as well. Thus, if F is given by (0.5), only (H1) need be assumed.

Our main results can now be stated.

Theorem A. *If (H1)–(H4) hold, then every orbit beginning in S^*_{n-1} is attracted either to p or to a nontrivial periodic orbit. If* $\mathrm{Diag}(p)\,\mathrm{DF}(p)$ *has more than one eigenvalue with positive real part, equivalently, if p is unstable for (0.1) in the linear approximation on S_{n-1}, then (0.1) has a nontrivial periodic orbit. If F is analytic on* $\mathrm{Int}\,\mathbb{R}^n_+$*, then there can be at most finitely many periodic orbits in S^*_{n-1} and at least one of these is orbitally asymptotically stable if p is linearly unstable.*

A corollary of Theorem A is as follows.

Corollary. *If F is given by (0.5) with $a_i = 0$, then for $n \leqslant 4$, p is a global attractor on S^*_{n-1}. If $n \geqslant 5$, then p is unstable and there exists an orbitally asymptotically stable periodic orbit in S^*_{n-1}.*

The first assertion of the corollary is known. See Ref. 7 (12.6). The second assertion had been conjectured in Ref. 10. For interesting work related to this conjecture see Refs. 2 and 9.

The remarkable fact about Theorem A is that it is not proved by studying solutions of (0.1) at all but rather by considering solutions of a related system on $\mathbb{R}^n_+$ given by

$$\dot{y}_i = y_i[F_i(y_i, y_{i-1}) - K] \tag{0.7}$$

where

$$K = \sum p_i F_i(p_i, p_{i-1}) = F_j(p_j, p_{j-1})$$

Our hypotheses (H1)–(H4) imply that (0.7) is a cooperative and irreducible system [4, 5, 12] as well as a monotone cyclic feedback system [8] on $\mathbb{R}^n_+$. Note also that p is an equilibrium of (0.7). The relationship between (0.1) and (0.7) is simple and we give it here. Let $y(t)$ be a solution of (0.7) with $y(0) \in \operatorname{Int} \mathbb{R}^n_+$. By a solution of (0.7), we always mean a solution maximally extended in the forward direction. Then $y(t)$ remains in the interior of $\mathbb{R}^n_+$ for $t > 0$ and a simple computation shows that

$$z(t) = Q[y(t)] \equiv y(t) \Big/ \sum y_i(t) \in S^*_{n-1}$$

satisfies the equation

$$\dot{z}_i = \pi(t)\, z_i \left[F_i(z_i, z_{i-1}) - \sum z_j F_j(z_j, z_{j-1}) \right] \tag{0.8}$$

where

$$\pi(t) = \left[\sum y_i(t) \right]^q$$

As $\pi(t)$ is positive, $z(t)$ traces out a portion of the positive orbit of (0.1) through $z(0)$. It is important to point out here that while solutions of (0.1) are globally defined due to the compactness of S^*_n, solutions of (0.7) need not be. If $y(t)$ has maximal interval of existence $[0, \tau)$ where $0 < \tau \leqslant \infty$, then the range of $z(t)$, defined above, is $\{x(s): 0 \leqslant s < \sigma\}$, where $x(s)$ is the solution of (0.1) satisfying $x(0) = z(0)$ and $\sigma = \int_0^\tau \pi(t)\, dt$. In general, the range of $z(t)$ is only a portion of the positive orbit of (0.1) through $z(0)$. Observe that if $\sum y_i(t)$ is bounded from above and from below, then $\tau = \infty$ and the range of $z(t)$ is the entire positive orbit of (0.1) through $z(0)$.

As (0.1) is assumed to be permanent, the orbit of (0.1) through $z(0)$ has compact closure B in S^*_{n-1}. This implies that the solution $y(t)$ of (0.7) lies in the cone over B described by $C = \{x \in \mathbb{R}^n_+ : x = sv \text{ for some } s \geqslant 0 \text{ and } v \in B\}$. In particular, if the orbit of (0.7) through $y(0)$ is bounded and bounded away from the origin, then this orbit has compact closure in $\operatorname{Int} \mathbb{R}^n_+$. Our assumptions (H3) and (H4) imply that (0.7) has exactly one equilibrium, namely, $y = p$, in $\operatorname{Int} \mathbb{R}^n_+$, and hence we may apply a modified version of Theorem 4.1 [8] to the solution $y(t)$ to conclude that it is asymptotic either to p or to a periodic orbit in $\operatorname{Int} \mathbb{R}^n_+$. Thus we can exploit the permanence of (0.1) to describe the asymptotic behavior of certain solutions of (0.7). We will be able to return the favor, that is, we show that there exists an invariant $n-1$-manifold M for (0.7) and a Lipschitz homeomorphism from M onto S^*_{n-1}, establishing a topological conjugacy between orbits of (0.1) and those of (0.7). M is the boundary of the basin of attraction of the origin for (0.7) in Int $\mathbb{R}^n_+$ if $K>0$. Theorem A is proved by using results from Ref. 8 applied to (0.7) on M.

In order to clarify the implications of the assumption (0.3) for (0.1), we introduce some additional notation. Following Ref. 3, (0.1) may be written as

$$\dot{x} = f(x) - [e^* f(x)]\, x \tag{0.9}$$

where

$$f_i(x) = x_i F_i(x)$$
$$e = (1, 1,..., 1)^*$$

and u^* denotes the transpose of the vector $\mathbf{u}$.

Similarly (0.7) becomes

$$\dot{y} = f(y) - Ky \tag{0.10}$$

The Jacobian of (0.10) at $y = p$ is given by $\mathrm{Diag}(p)\,\mathrm{DF}(p)$. Writing $J(p)$ for the Jacobian of the right-hand side of (0.9) at $x = p$, direct calculation, using the homogeneity of F, gives the following:

$$\mathrm{Df}(p)\, p = (q+1)\, Kp$$
$$\mathrm{Diag}(p)\,\mathrm{DF}(p) = \mathrm{Df}(p) - KI$$
$$J(p) = \mathrm{Diag}(p)\,\mathrm{DF}(p) - pe^*[\mathrm{Diag}(p)\,\mathrm{DF}(p) + KI]$$
$$J(p)\, p = -Kp, \qquad e^* J(p) = -Ke^*$$

It follows that Kq is an eigenvalue of $\mathrm{Diag}(p)\,\mathrm{DF}(p)$ with corresponding eigenvector p. As $\mathrm{Diag}(p)\,\mathrm{DF}(p)$ is an irreducible matrix with nonnegative off-diagonal entries, by (H2), the Perron–Frobenius theorem, together with the positivity of p, implies that Kq is a simple eigenvalue which is strictly larger than the real part of all other eigenvalues of $\mathrm{Diag}(p)\,\mathrm{DF}(p)$. Straightforward calculations as in Ref. 3 show that $\mathrm{Diag}(p)\,\mathrm{DF}(p)$ and $J(p)$ share $n-1$ common eigenvalues. Indeed, if $\lambda \neq Kq$ is an eigenvalue of $\mathrm{Diag}(p)\,\mathrm{DF}(p)$ with corresponding eigenvector u, then λ is an eigenvalue of $J(p)$ with corresponding eigenvector $u - (e^* u)\, p$. Hence the stability of the equilibrium $x = p$ for (0.1) on S_{n-1} is determined by the $n-1$ eigenvalues of $\mathrm{Diag}(p)\,\mathrm{DF}(p)$ distinct from Kq, whereas $-K$ is the eigenvalue at p transversal to S_{n-1}.

In particular, (0.3) means precisely that p is a nondegenerate equilibrium for (0.1), i.e., the eigenvalues of $J(p)$ are nonzero (and $K \neq 0$).

If $K<0$, then the remaining $n-1$ eigenvalues have negative real part, and p is linearly stable for (0.7) on Int $\mathbb{R}_+^n$ as well as for (0.1) on S_{n-1}. As we show in Lemma 1.1, p is actually globally stable in this case.

If $K>0$, then some eigenvalues may have nonnegative real part. However, (H1) and the index theorem in Ref. 7 (Chap. 19.3) imply that the number of eigenvalues of $J(p)$ with positive real part must be even. Hence, for $K>0$, (0.3) can be improved to

$$\mathrm{Det}[-\mathrm{DF}(p)]<0 \tag{0.11}$$

or, after evaluation,

$$\Pi\left(-\frac{\partial F_i}{\partial x_i}\right)<\Pi\left(\frac{\partial F_i}{\partial x_{i-1}}\right) \tag{0.12}$$

Hence, if $K>0$, $\mathrm{Diag}(p)\,\mathrm{DF}(p)$ has an odd number of eigenvalues with positive real part.

The following notation is used. We write $x \leqslant y$ for vectors x and y provided that $x_i \leqslant y_i$ holds for every i and we write $x \ll y$ if the strict inequality $x_i < y_i$ holds for each i. If $x \leqslant y$, then $[x, y]$ is the set of vectors $\mathbf{z}$ satisfying $x \leqslant z \leqslant y$. If A and B are subsets of $\mathbb{R}^n$, then $A \leqslant B$ $(A \ll B)$ means that $a \leqslant b$ $(a \ll b)$ holds for every choice of $a \in A$ and $b \in B$. We write $\omega(z)$ for the omega (positive) limit of a point z and $\alpha(z)$ for the alpha (negative) limit set of z.

Recall that if y and z are initial conditions for a cooperative and irreducible system such as (0.7) and if $y \leqslant z$, $y \neq z$, then $y(t) \ll z(t)$ holds for all $t>0$, where $y(t)$ and $z(t)$ are the solutions of (0.7) satisfying $y(0)=y$ and $z(0)=z$. This property of solutions of (0.7) is referred to as the strong monotonicity property. See Refs. 4–6 and 12 for further details.

1. PROOF OF THEOREM A

In this section we establish our main result by studying the asymptotic behavior of the system (0.7) on $\mathbb{R}_+^n$, assuming throughout that (H1)–(H4) hold. Note that the homogeneity of the F_i, or (0.8), implies that the ray through p, $\{sp\colon s \geqslant 0\}$, is invariant with dynamics

$$\dot{s}=Ks(s^q-1) \tag{1.1}$$

Using (H3), one easily shows that p is the only equilibrium point in Int $\mathbb{R}_+^n$, if $K \neq 0$.

We first treat the trivial case $K<0$.

Lemma 1.1. *If $K < 0$, then p is a globally stable equilibrium for (0.7) on* Int $\mathbb{R}^n_+$ *[and therefore for (0.1) on S^*_{n-1}].*

Proof. In this case, since $F(0) = 0$, 0 is repelling. But (1.1) shows that solutions on the invariant ray through p converge monotonically to p as t tends tò infinity. For any $y \in \text{Int } \mathbb{R}^n_+$ we can choose $0 < r < 1 < s$ such that $y_1 \equiv rp \leqslant y \leqslant sp \equiv y_2$. Then, by monotonicity, $y_1(t) \leqslant y(t) \leqslant y_2(t)$ for all $t \geqslant 0$, and hence $y(t) \to p$ as $t \to \infty$. ▌

For the rest of the paper we assume $K > 0$. In this case the origin is an attracting equilibrium for (0.7) and p is either a saddle point or a repellor. We write $[0, \tau)$ for the maximal interval of existence of a solution $y(t)$ of (0.7), where τ depends on $y(0)$ and $0 < \tau \leqslant \infty$. From (1.1), p repels solutions on the invariant ray through p, which coincides with the "most unstable manifold" of p [12]. By simple comparison with solutions on this ray, we obtain the following result on the basins of attraction of the equilibria 0 and ∞, defined as

$$B(0) = \{ y \in \mathbb{R}^n_+ : \lim_{t \to \infty} y(t) = 0, \text{ where } y(0) = y \}$$

$$B(\infty) = \left\{ y \in \mathbb{R}^n_+ : \lim_{t \to \tau} \sum y_i(t) = \infty, \text{ where } y(0) = y \right\}$$

Lemma 1.2.

(a) *If $y \in B(0)$, then* $[0, y] \subset B(0)$.

(b) $[0, p] - \{p\} \subset B(0)$.

(c) $[p, \infty] - \{p\} \subset B(\infty)$.

For the proof of (b) and (c), one uses the strong monotonicity of the flow.

Integration of (1.1) reveals that solutions of (0.7) beginning on the invariant ray through p and larger than p blow up in finite time ($\tau < \infty$). By comparison with such a solution, it follows from Lemma 1.3(d) that every point of $B(\infty)$ has finite escape time, τ.

Finally, we may define the analog of S_{n-1} for (0.7). Let

$$M = \text{boundary of } B(0) \text{ relative to Int } \mathbb{R}^n_+$$

The following lemma is closely related to a result in Ref. 6.

Lemma 1.3. *M has the following properties.*

(a) *M is an invariant set for (0.7) containing $y = p$.*

(b) *M does not contain distinct points y and z such that $y \leqslant z$.*

(c) *Every ray* $\{tv: t \geqslant 0\}$, $v \in S^*_{n-1}$, *intersects* M *exactly once.* M *is Lipschitz homeomorphic to* S^*_{n-1}.

(d) *Every positive orbit beginning on* M *has compact closure in* M. *On the other hand,* $y(0) \in \operatorname{Int} \mathbb{R}^n_+$ *belongs to an unbounded forward orbit if and only if* $\lim_{t \to \tau} y_i(t) = \infty$ *for each* i. *Thus,* $B(\infty) = \{y: y_i(t) \to \infty$ *as* $t \to \tau$ *for each* $i\}$.

(e) *The flow of (0.7) on* M *is topologically equivalent to the flow of (0.1) on* S^*_{n-1}. *In particular, (0.7) possesses a compact attractor on* M.

Proof. The invariance of M is immediate from its definition and p belongs to M by Lemma 1.2(b). If $y(0)$ and $z(0)$ belong to M and $y(0) \leqslant z(0)$, then $y(t) \ll z(t)$ for $t > 0$ by strong monotonicity. Hence we may find $u(1) \in B(0)$ close to $z(0)$. But this implies that $y(1) \ll u(1)$ and hence $y(1) \in B(0)$ by Lemma 1.2(a), a contradiction. Thus (b) holds and the uniqueness of the intersection of a ray with M follows. To see that the ray actually intersects M, observe that $(tv) \gg p$ for sufficiently large t and such (tv) do not belong to $B(0)$. On the other hand (tv) belongs to $B(0)$ for small t by Lemma 1.2. It follows that the ray intersects M. Hence an injective map is defined from S^*_{n-1} onto M by assigning to each $v \in S^*_{n-1}$ the unique point of intersection of the ray through v with M. This map can be shown to be Lipschitz continuous and its inverse, Q restricted to M, is also Lipschitz continuous. See Ref. 6 for more details.

We now turn to assertion (d). Let $y(0) \in \operatorname{Int} \mathbb{R}^n_+$ and suppose that $y(t)$ is defined for $t \in [0, \tau)$, $0 < \tau \leqslant \infty$. Suppose also that there exists $m > 1$ such that for each $t \in [0, \tau)$ we have $y_i(t) \leqslant mp_i$ for some i, where p is the equilibrium. We claim that $y(t)$ is bounded as $t \to \tau$. If not, then $Y(t) = \sum y_i(t)$ is unbounded and hence $\liminf_{t \to \tau} z_i(t) = 0$ for some value of i, where $z(t) = y(t)/Y(t)$. But this contradicts that (0.1) is permanent by the arguments given in Section 0. Thus if $y(0)$ belongs to $B(\infty)$, then for each $m > 1$ there exists $s \in [0, \tau)$ such that $y(s) \gg mp$. But then $y(t) \gg mp$ for $s \leqslant t < \tau$ by monotonicity and the fact that the ray through p is an orbit of (0.7). On the other hand, if $y(0) \in M$, then $y(t)$ is bounded since no point of M can be related to p except p itself. This proves (d).

Earlier arguments established that if $y(0) \in M$, then Q maps the orbit of $y(0)$ onto the orbit of (0.1) through $Qy(0)$, preserving the direction of the flow. Indeed, if $y(0) \in M$, then $\sum y_i(t)$ is bounded from above and from below, so that from our remarks following (0.8) in Section 0, the range of $z(t) = Q[y(t)]$ coincides with the positive orbit of (0.1) through $z(0)$. This establishes the equivalence of the flows. The existence of a compact attractor for (0.7) on M follows from the fact that (0.1) is permanent on S_{n-1} and thus there exists a compact attractor for (0.1) on S_{n-1}^*. This proves (e). ■

Theorem 1.4. *The forward orbit of a point on M approaches either p or a nontrivial periodic orbit.*

Proof. This follows immediately from Lemma 1.3(d), (0.11), and Theorem 4.1 of Ref. 8. Note that (0.7) has equilibria on the boundary of the nonnegative cone so Theorem 4.1 does not immediately apply. However, since the closure of the orbit is compact in M and M contains only the equilibrium p, the arguments yielding Theorem 4.1 apply here. Observe that (0.11) is precisely (4.5) in Ref. 8 (Theorem 4.1). ■

We remark that all periodic orbits of (0.7) are linearly unstable, i.e., every such orbit has one real Floquet multiplier larger than one by Lemma 1.2 of Ref. 11.

Our next result describes the possible asymptotic behavior of orbits of (0.7) not on M.

Lemma 1.5. Int $\mathbb{R}^n_+ \subset B(0) \cup M \cup B(\infty)$.

Proof. Suppose $y(0)$ does not belong to $B(0)$, M, or $B(\infty)$. Then the forward orbit through $y(0)$ is bounded and hence has compact closure in Int $\mathbb{R}^n_+$. Its limit set is either p or a nontrivial periodic orbit by the same reasoning as in the previous theorem. In any case there exists $r \in (0, 1)$ such that $y_1 = ry(0) \in M$. From (0.8) we know that $y(t) = s(t)\, y_1[\tau(t)]$, where $s(t) > 1$ and $\tau(t)$ is a monotonically increasing reparameterization of time. If $y_1(t) \to p$ as $t \to \infty$, then also $y(t) \to p$ as $t \to \infty$, since p is the only possible limit set on the ray $\{rp: r > 0\}$. But then all solutions starting in the interval $[y_1, y]$ are attracted to p, so that p is a "trap" in the terminology of Ref. 5. But this implies that the leading eigenvalue at p is nonpositive, which contradicts $K > 0$.

If $\omega(y_1)$ is a periodic orbit γ_1, then $\omega(y) = \gamma_2$ is a periodic orbit on the cone C spanned by γ_1 from the apex 0. As noted above, each of these periodic orbits is linearly unstable and its "most unstable manifold," constructed in Ref. 11, is contained in the cone C by (0.8). This implies $\gamma_1 = \gamma_2$. But this contradicts the limit set dichotomy of Ref. 5, which says $\gamma_1 \ll \gamma_2$. ■

Lemma 1.6. *If γ is a nontrivial periodic orbit on M and $W^s(\gamma)$ is its stable manifold, then $W^s(\gamma) \subset M$. Similarly, $W^s(p) \subset M$.*

Proof. If $y(0)$ belongs to $W^s(\gamma) - M$, then by Lemma 1.5 either $y(0) \in B(0)$ or $y(0) \in B(\infty)$, either of which are contradictions. Similar reasoning leads to the other conclusion. ■

Theorem 1.7. *If* Diag(p) DF(p) *has more than one eigenvalue with positive real part, then there exists a relatively open, positively invariant subset U of M such that the limit set of the orbit of every point of U is a nontrivial periodic orbit.*

Proof. The Jacobian of (0.7) at $y = p$ is given by Diag(p) DF(p). Thus (0.11) implies that Det$[-\text{Diag}(p)\,\text{DF}(p)] < 0$. In particular, the Jacobian has an odd number of eigenvalues with positive real part. As we assume that there is more than one such eigenvalue, it follows that there are at least three. We can now apply the ideas of Theorem 4.1 in Ref. 8 together with Remark 4.4 in that paper. Let

$$U = \{y \in M \cap \mathcal{N} : N(y - p) = 2\}$$

where N is the integer-valued function defined as $N(z) = \#\{i: z_i z_{i-1} < 0\}$ in the aforementioned paper and $\mathcal{N}$ is its domain. As $\mathcal{N}$ is open and N is continuous on $\mathcal{N}$, it is clear that U is open in M. Furthermore, U is positively invariant. Indeed, since N can only decrease along a forward trajectory and since it assumes only even values, it follows that if $y(0) \in U$, then either $N[y(t) - p] = 2$ holds for all $t > 0$ or $N[y(t) - p] = 0$ must hold for all large $t > 0$. But the latter means that either $y(t) \gg p$ or $y(t) \ll p$ holds for all large values of t. Hence, either $y(0) \in B(0)$ or $y(t) \to \infty$, by Lemma 1.2. In any case we have a contradiction and this proves that U is positively invariant. In order to see that U is not empty, let $z = (p_1, lp_2, lp_3, ..., lp_n)$, where $l > 1$ so $z \gg p = (p_1, p_2, ..., p_n)$. Then there exists a unique $r > 0$ such that $rz \in M$ by Lemma 1.3. Clearly $r < 1$ since the orbit through z is unbounded by Lemma 1.2. But $rlp_i > p_i$ must hold for some $i \geq 2$ or else $rz \in B(0)$ by Lemma 1.2. It follows that $rl > 1$ and this easily implies that $N(rz - p) = 2$. Thus $rz \in U$.

If $y(0) \in U$, then $y(t)$ tends to a nontrivial periodic orbit as $t \to \infty$ by Theorem 4.1 and Remark 4.4 of Ref. 8. ∎

Proposition 1.8. *If F is analytic in* Int $\mathbb{R}^n_+$, *then there are at most finitely many periodic orbits on M.*

Proof. The proof is essentially identical to the proof of Theorem 4.3 in Ref. 8. The permanence of (0.1) implies that (0.7) has a compact attractor A on M, that is, A is a compact subset of M which contains the positive limit set of all orbits of points of M. The attractor A provides the compact attracting set required in the hypotheses of Theorem 4.3 mentioned above. Observe that the proof of the assertion in Theorem 4.3 that there are at most finitely many periodic orbits did not use the hypothesis that Df(x_*) has at least two eigenvalues with positive real part. ∎

Proposition 1.9. *Assume that the hypotheses of Theorem 1.7 and Proposition 1.8 hold. Then there exists an orbitally asymptotically stable periodic orbit of (0.7).*

Proof. Let U be the open subset of M identified in Theorem 1.7. We will show that U contains an orbitally asymptotically stable periodic orbit by an indirect argument. Assume that no such periodic orbits exist in U. Observe that U is positively invariant and contains the positive limit set of every orbit beginning in U. Every such limit set is a nontrivial periodic orbit by Theorem 1.7, and furthermore, U contains only finitely many periodic orbits by Proposition 1.8.

Let γ be a periodic orbit of (0.7) in U. By the theory in Ref. 8, if $\{\alpha_k\}_{k=1}^{n}$ are the Floquet multipliers of γ ordered such that $\sigma_k \geqslant \sigma_{k+1}$, where $\sigma_k = |\alpha_k|$ and $\mathscr{G}_\sigma$ is the real part of the direct sum of the generalized eigenspaces of the period map (Poincaré map) associated with the linearized equation about γ corresponding to all Floquet multipliers α with $\sigma = |\alpha|$, then we have

$$\sigma_1 > \sigma_2 \geqslant \sigma_3 > \sigma_4 \geqslant \sigma_5 > \cdots > \sigma_{n-1} \geqslant \sigma_n, \qquad \sigma_1 = \alpha_1 > 1$$

and

$$N = 0 \text{ on } \mathscr{G}_{\sigma_1}, \qquad N = 2h \text{ on } \mathscr{G}_{\sigma_{2h}} + \mathscr{G}_{\sigma_{2h+1}} \text{ for } h = 1, 2, ..., b-1 \tag{1.2}$$

where $n = 2b - 1$ is odd, $\mathscr{G}_{\sigma_1}$ is one-dimensional and $\mathscr{G}_{\sigma_{2h}} + \mathscr{G}_{\sigma_{2h+1}}$ is two-dimensional. Furthermore, $\alpha_{2h}\alpha_{2h+1} > 0$. When n is even, then

$$\sigma_1 > \sigma_2 \geqslant \sigma_3 > \sigma_4 \geqslant \sigma_5 > \cdots > \sigma_{n-2} \geqslant \sigma_{n-1} > \sigma_n, \qquad \sigma_1 = \alpha_1 > 1$$

and, in addition to (1.2) and the above, $N = n$ on $\mathscr{G}_{\sigma_n}$, which is one-dimensional and $\alpha_n > 0$.

If U contains a periodic orbit γ with $\sigma_2 = \alpha_2 = 1$ and $\sigma_3 < 1$, then γ is hyperbolic and $W^s(\gamma)$ is an $n-1$-dimensional manifold contained in M by Lemma 1.6. In this case, γ is orbitally asymptotically stable on M in contradiction to our hypothesis. But U contains at least one periodic orbit γ which attracts an open subset of U. For such an orbit it must be the case that $\alpha_2 = \alpha_3 = 1$ and that $\sigma_4 < 1$, since γ cannot be hyperbolic. Thus γ has a two-dimensional center manifold, $W^c(\gamma)$, which is homeomorphic to $(-1, 1) \times S^1$. As γ is an isolated periodic orbit, solutions of (0.7) beginning at $z \in W^c(\gamma)$ sufficiently close to γ either spiral toward $[\omega(z) = \gamma]$ or away from $[\alpha(z) = \gamma]\gamma$. If γ attracts all orbits beginning on $W^c(\gamma)$ sufficiently near γ, then γ is orbitally asymptotically stable on $W^{cs}(\gamma)$. In this case, $W^{cs}(\gamma)$ is an $n-1$-dimensional manifold contained in M, by arguing as in

Lemma 1.6. It follows that γ is orbitally asymptotically stable on M in contradiction to our hypothesis. Returning to our periodic orbit γ which attracts an open subset of U, if $\alpha(z)=\gamma$ for all z on $W^c(\gamma)$ sufficiently near to γ, then γ cannot attract an open subset of U. Hence γ must be a saddle-node orbit for the flow restricted to $W^c(\gamma)$.

In order to be more precise we introduce some ideas from Ref. 8. There it is shown that if Π_i is the projection of $\mathbb{R}^n$ onto the (x_i, x_{i-1}) plane defined by $\Pi_i x=(x_i, x_{i-1})$, then Π_i, restricted to $W^c(\gamma)$, is a diffeomorphism onto its range and $\Pi_i\gamma$ is a closed Jordan curve in $\mathbb{R}^2$. $W^c(\gamma)$ is homeomorphic to $(-1, 1)\times S^1$ so we may choose coordinates such that

$$\gamma=\{0\}\times S^1$$
$$\Pi_i[(-1, 0)\times S^1]\subset(\Pi_i\gamma)_{\text{int}}$$
$$\Pi_i[(0, 1)\times S^1]\subset(\Pi_i\gamma)_{\text{ext}}$$

where "int" and "ext" refer to the interior, respectively, exterior component of $\mathbb{R}^2-\Pi_i\gamma$. We say that γ is attracting (repelling) from the exterior on $W^c(\gamma)$ provided that $\omega(z)=\gamma$ $[\alpha(z)=\gamma]$ for all $z\in(0, 1)\times S^1$. The notion of attracting and repelling from the interior on $W^s(\gamma)$ are similarly defined with $(-1, 0)\times S^1$. In Ref. 8 we observe that distinct periodic orbits γ_1 and γ_2 are such that $\Pi_i\gamma_1$ and $\Pi_i\gamma_2$ do not intersect and that $\Pi_i p$ is contained in $(\Pi_i\gamma)_{\text{int}}$ for every nontrivial periodic orbit γ. Furthermore, there is a partial ordering on the set of periodic orbits on M (or on U) as follows: $\gamma_1<\gamma_2$ if $\Pi_i\gamma_1\subseteq(\Pi_i\gamma_2)_{\text{int}}$.

Consider now a periodic orbit, γ, in U which attracts an open subset of U. By our hypotheses, γ is a saddle-node orbit with respect to the flow restricted to $W^c(\gamma)$. We assume that γ is attracting from the interior and repelling from the exterior on $W^c(\gamma)$. The argument is similar if the reverse is true. Since there are only finitely many periodic orbits in U, we may assume that γ is maximal, with respect to the partial ordering defined above, among all orbits in U possessing the following properties: (1) γ has a two-dimensional center manifold on which γ is attracting from the interior and repelling from the exterior, and (2) $\sigma_4<1$. By Lemma 1.6 or, more accurately, by the ideas in the proof of Lemma 1.6, it follows that the portion of $W^c(\gamma)$ described by $(-1, 0)\times S^1$ belongs to M, since all orbits on it tend to γ as t increases. Consider $(0, 1)\times S^1$, which, in general, may not belong to M. If $[(0, 1)\times S^1]\subseteq U$ and $z\in(0, 1)\times S^1$, then $\alpha(z)=\gamma$ and $\omega(z)=\gamma^*$, where γ^* is a periodic orbit in U, by Theorem 1.7. Arguing as in Ref. 8 (Theorem 4.2), one shows that if $\mathcal{O}(z)$ is the entire orbit through z, then $N(z_1-z_2)=2$ whenever z_1, z_2 are distinct points of the closure of

$\mathcal{O}(z)$. Indeed, by Lemma 3.9 of Ref. 8, $N[z(t)-z(s)]=2$ whenever $t \neq s$ are sufficiently negative. As $N[z(t+r)-z(s+r)]$ is nonincreasing in r, it follows that either $N[z(t+r)-z(s+r)]=2$ holds for all r or the value zero is attained for all large r. But the latter implies that $z(t+r) \ll z(s+r)$, or the reverse inequality holds for all large r. This, in turn, implies that $z(t)$ converges to an equilibrium as $t \to \infty$ by the convergence criteria of Refs. 4 and 5, and since this is impossible, we have that $N[z(t+r)-z(s+r)]=2$ for all r. Hence our claim is established. In particular, this implies that $\gamma \neq \gamma^*$, that is, the orbit through z is not a homoclinic orbit to γ but, in fact, is a heteroclinic orbit connecting distinct periodic orbits satisfying $\gamma < \gamma^*$. Furthermore, if $z(t)$ is the solution of (0.7) satisfying $z(0)=z$, then $z(t)$ approaches γ^* along $W^{cs}(\gamma^*)$. It follows that N attains the value 2 on some $\mathcal{G}_\sigma$ for the variational equation about γ^* with $\sigma \leqslant 1$. Hence arguments parallel to those in Ref. 8 (Theorem 4.2) show that $\alpha_2 = \alpha_3 = 1$ (recall that σ_3 cannot be less than one, for then γ^* is orbitally asymptotically stable on U, contrary to our assumption). It follows that γ^* has a two-dimensional center manifold which is attracting from the interior. Since γ^* cannot be orbitally asymptotically stable on U, γ^* must be repelling from the exterior on its center manifold. This gives a contradiction to the assumed maximality of γ in U with the properties (1) and (2).

Now suppose that $(0, 1) \times S^1$ is not contained in U. One can argue as in Lemma 1.5 that for each $z' \in (0, 1) \times S^1$ there exists $z \in U$ on the ray through z' such that $z(t) = s(t)\, z'(\tau(t))$ holds for all t in their common domain, where $s(t) > 1$ or $s(t) < 1$ holds for all t. As in Lemma 1.5, it follows that $z(t) - z'(t) \to 0$ as $t \to -\infty$. As $z(t)$ approaches γ along its center unstable manifold as $t \to -\infty$ and $z(t)$ cannot be related to a point of γ by $\ll$, it follows that there exists $T > 0$ such that whenever $t < -T$, $s < -T$ and $t \neq s$, then $N[z(t)-z(s)]=2$ and $N[z(t)-\gamma]=2$. Using the fact that $N[z(t+r)-z(t)]$ is nonincreasing in t for each $r \neq 0$ and that no two points of the orbit through z can be related by $\ll$, one sees that $N(z_1 - z_2) = 2$ whenever z_1, z_2 are distinct points of the closure of $\mathcal{O}(z)$. It follows that $\Pi_i \mathcal{O}(z)$ does not meet $\Pi_i \gamma$. Now $\Pi_i z'(t)$ approaches $\Pi_i \gamma$ from $(\Pi_i \gamma)_{\text{ext}}$ as $t \to -\infty$ since z' belongs to $(0, 1) \times S^1$. Hence, there exists t_1 and t_2 such that $\Pi_i z'(t_1) \ll \Pi_i \gamma$ and $\Pi_i z'(t_2) \gg \Pi_i \gamma$, where the inequalities are componentwise in $\mathbb{R}^2$. But $s(t)\, z'[\tau(t)] = z(t)$ implies that $\Pi_i z'(t_2) \ll \Pi_i z[\tau^{-1}(t_2)]$, if $s > 1$, or $\Pi_i z[\tau^{-1}(t_1)] \ll \Pi_i z'(t_1)$, if $s < 1$. We note here that the projections have positive coordinates. In either case, it follows that $\Pi_i \mathcal{O}(z) \subset (\Pi_i \gamma)_{\text{ext}}$. Now $z(t)$ tends to a periodic orbit γ^* in U as $t \to \infty$, by Theorem 1.7. Arguing exactly as in the paragraph above, we obtain that $\gamma < \gamma^*$ and that γ^* has the properties (1) and (2). This, again, is a contradiction to our assumption that γ is maximal with these properties and completes our proof. ■

Remark. Theorem A and the corollary follow from Lemma 1.3(e), Theorems 1.4 and 1.7, and Propositions 1.8 and 1.9.

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