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The Poincaré–Bendixson Theorem for Monotone Cyclic Feedback Systems

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We prove the Poincaré–Bendixson theorem for monotone cyclic feedback systems; that is, systems in $\mathbf{R}^n$ of the form

$$x_i = f_i(x_i, x_{i-1}), \qquad i = 1, 2, ..., n \ (\mathrm{mod}\ n).$$

We apply our results to a variety of models of biological systems.

KEY WORDS: Cellular control system; cyclic system; monotonicity; negative feedback; Poincaré–Bendixson theorem.

0. INTRODUCTION

In this paper we study systems of ordinary differential equations in $\mathbf{R}^n$, in which the n coordinate variables $x^1, x^2,..., x^n$, drive, or force one another in a cyclic fashion. To be precise, we consider systems of the form

$$\dot{x}^i = f^i(x^i, x^{i-1}), \qquad i = 1, 2,..., n \tag{0.1}$$

where we agree to interpret x^0 as x^n. [As there will be a frequent need to make such interpretations, due to the cyclic nature of the feedback in (0.1), let us agree that all indices (superscripts) of all variables are to be taken modulo n.] We assume the nonlinearity $f = (f^1, f^2,..., f^n)$ is defined on a nonempty open set $O \subset \mathbf{R}^n$ with the property that each coordinate projection $O^i \subset \mathbf{R}^2$ of O onto the (x^i, x^{i-1}) plane is convex and that $f^i \in C^1(O^i)$.

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Our key assumption about the cyclic system (0.1) is that the variable x^{i-1} forces $\dot{x}^i$ monotonically. We assume for some $\delta^i \in \{-1, +1\}$, that

$$\delta^i \frac{\partial f^i(x^i, x^{i-1})}{\partial x^{i-1}} > 0 \qquad \text{for all } (x^i, x^{i-1}) \in O^i \qquad \text{and } 1 \leqslant i \leqslant n \quad (0.2)$$

Thus δ^i describes whether the effect of x^{i-1} is to inhibit the growth of $x^i (\delta^i = -1)$ or to augment its growth $(\delta^i = +1)$. The product

$$\Delta = \delta^1 \delta^2 \cdots \delta^n$$

characterizes the entire system as one with negative feedback $(\Delta = -1)$ or positive feedback $(\Delta = +1)$. We term such a system, of the form (0.1), satisfying (0.2), *a monotone cyclic feedback system.*

Our main result, in essence, is that the Poincaré–Bendixson theorem holds for monotone cyclic feedback systems. In particular, the omega-limit set of any bounded orbit of a monotone cyclic feedback system can be embedded in $\mathbf{R}^2$ and must, in fact, be of the type encountered in two-dimensional systems: either a single equilibrium, a single nonconstant periodic solution, or a structure consisting of a set of equilibria together with homoclinic and heteroclinic orbits connecting these equilibria. Further, related results for linear systems severely restrict the type of bifurcations which can occur in such systems. Simple Hopf bifurcations and stationary bifurcations with null spaces of dimension at most two are possible, however, higher-dimensional bifurcations do not occur. Also excluded are period doubling bifurcations and bifurcations of periodic orbits to invariant tori. In a general sense "chaos" is ruled out.

Before stating our result precisely, we introduce a bit of notation. Letting $x_0 \in O \subset \mathbf{R}^n$ denote an initial condition $x(0) = x_0$ for a solution $x(t)$ of (0.1), we write for $T \in \mathbf{R}$ the semiorbits

$$\gamma^{T+}(x_0) = \{x(t) \mid t \geqslant T \text{ and } t \in \operatorname{dom} x(\cdot)\},$$
$$\gamma^{T-}(x_0) = \{x(t) \mid t \leqslant T \text{ and } t \in \operatorname{dom} x(\cdot)\},$$
$$\gamma^{\pm}(x_0) = \gamma^{0\pm}(x_0),$$

and denote the orbit

$$\gamma(x_0) = \gamma^+(x_0) \cup \gamma^-(x_0).$$

We let $\alpha(x_0)$ and $\omega(x_0)$ denote the usual alpha- and omega-limit sets of $\gamma(x_0)$, provided of course the solution $x(t)$ exists as $t \to -\infty$ or $+\infty$. If γ is an equilibrium or periodic orbit, we denote by W^s, W^{cs}, W^c, W^{cu}, and W^u the stable, center-stable, center, center-unstable, and unstable manifolds, respectively of γ; these arise in later sections of the paper. Finally, we let $\Pi^i\colon \mathbf{R}^n \to \mathbf{R}^2$ denote, for each i, the coordinate projection

$$\Pi^i x = (x^i, x^{i-1})$$

We now give our main result.

Main Theorem. *(a) Let $x(t)$ be a solution of the monotone cyclic feedback system (0.1), (0.2), through $x(0) = x_0$, and suppose the forward orbit $\gamma^+(x_0)$ is bounded, with closure $\overline{\gamma^+(x_0)} \subset O$. Then the omega-limit set $\omega(x_0)$ is one of the following:*

(i) an equilibrium y_0,

(ii) a nonconstant periodic orbit, or

(iii) a set $E \cup H$ where each $y_0 \in E$ is an equilibrium at which $\Delta \det(-Df(y_0)) \geqslant 0$, with $\Delta = \prod_{i=1}^n \delta^i$, and where H is a set of orbits homoclinic to/heteroclinic between points of E; that is, if $y_0 \in H$, then $\alpha(y_0) = \{z_0\}$ and $\omega(y_0) = \{w_0\}$ for some z_0, $w_0 \in E$. There, moreover, exists an integer k_∞, which is odd if $\Delta = -1$ and even if $\Delta = +1$, such that for each $z_0 \in E$ the matrix $Df(z_0)$ has either $k_\infty - 1$ or k_∞ eigenvalues γ satisfying $Re\,\gamma > 0$.

(b) For each i the planar projection

$$\prod{}^i\colon \omega(x_0) \to \mathbf{R}^2 \tag{0.3}$$

is one-to-one on the omega limit set. In fact, in cases (i) and (iii) (that is, where $\omega(x_0)$ is not a nonconstant periodic orbit) there exist $T \geqslant 0$ such that for each i the projection

$$\prod{}^i\colon \overline{\gamma^{T+}(x_0)} = \gamma^{T+}(x_0) \cup \omega(x_0) \to \mathbf{R}^2 \tag{0.4}$$

is one-to-one on the forward orbit closure.

(c) In any case (i), (ii), or (iii) there exists $T \geqslant 0$ such that if $y_0 \in \gamma^{T+}(x_0)$ is not an equilibrium, then the projection of the vector field through that point is nonzero

$$\Pi^i \dot{y}(0) = (f^i(y_0), f^{i-1}(y_0)) \neq (0, 0) \tag{0.5}$$

We note that in case (ii), when $\omega(x_0)$ is a periodic orbit, that while the omega-limit set projects homomorphically onto the plane (0.3), the projection of the forward orbit closure (0.4) need not be one-to-one for any

$T \geqslant 0$. Indeed, the linear equation $x^{(6)} + x = 0$, written as the monotone cyclic feedback system

$$\begin{aligned} \dot{x}^1 &= -x^6 \\ \dot{x}^i &= x^{i-1}, \qquad 2 \leqslant i \leqslant 6 \end{aligned} \tag{0.6}$$

in $\mathbf{R}^6$ [here $x^i = x^{(6-i)}$ for $1 \leqslant i \leqslant 6$], exhibits this phenomenon. Consider the solution of (0.6), whose first two coordinates are

$$\begin{aligned} x^2(t) &= \sin t + e^{-\alpha t} \sin \beta t \\ x^1(t) &= \dot{x}^2(t) = \cos t + e^{-\alpha t}(\beta \cos \beta t - \alpha \sin \beta t) \end{aligned}$$

with $x^i(t)$, $3 \leqslant i \leqslant 6$, defined uniquely by (0.6), and with

$$\alpha = \tfrac{1}{2}\sqrt{3}, \qquad \beta = \tfrac{1}{2}$$

corresponding to the eigenvalues $-\alpha \pm i\beta$ of the differential equation. Clearly, the projection of the omega-limit set of this orbit onto the (x^2, x^1)-plane is the circle

$$\Pi^2 \omega(x_0) = \{(x^2, x^1) \in \mathbf{R}^2 \mid (x^2)^2 + (x^1)^2 = 1\}$$

We claim the projection $\Pi^2 x(t) = (x^2(t), x^1(t))$ of the orbit crosses this circle infinitely often as $t \to \infty$. Indeed,

$$(x^2(t))^2 + (x^1(t))^2 - 1 = e^{-\alpha t} p(t) + O(e^{-2\alpha t})$$

where $p(t)$ is the 4π-periodic function

$$p(t) = 2(\sin t \sin \beta t + \beta \cos t \cos \beta t - \alpha \cos t \sin \beta t)$$

As $p(t)$ changes sign infinitely often (since $p(t + 2\pi) = -p(t) \not\equiv 0$), the claim is proved. It follows immediately from this that Π^2 is not one-to-one on $\overline{\gamma^{T+}(x_0)}$ for any T.

As mentioned above, there are really two fundamental types of monotone cyclic feedback systems (0.1), characterized by $\Delta = \delta^1 \delta^2 \cdots \delta^n$. It is not difficult to see that a change of variables $x^i \to \mu^i x^i$, where $\mu^i \in \{-1, +1\}$ are appropriately chosen, yields a monotone cyclic feedback system (0.1) where

$$\begin{aligned} \delta^i &= +1, \qquad 2 \leqslant i \leqslant n \\ \delta^1 &= \begin{cases} +1, & \text{if } \Delta = +1 \\ -1, & \text{if } \Delta = -1 \end{cases} \end{aligned} \tag{0.7}$$

One could think of (0.7) as a "canonical form" for such systems. It follows immediately that if $\Delta = +1$, then (0.1) is a cooperative and irreducible system in the sense of Hirsch [20–22] (see also Ref. 37) and the many results for monotone dynamical systems contained in the above mentioned work apply to (0.1). In particular, there is a strong tendency for solutions to converge to equilibria (see Refs. 20–22). If $\Delta = -1$, then (0.1) is not cooperative; it is a competitive system (see Ref. 37) if n is odd. Observe also that the time-reversed monotone cyclic feedback system (0.1) is again a monotone cyclic feedback system. In fact, time reversal has the effect of changing Δ to $(-1)^n \Delta$. Our focus is primarily on the case that $\Delta = -1$ since the range of possible dynamical behavior is not so restrictive in this case.

Monotone cyclic feedback systems arise in a variety of mathematical models of biological systems, for example, in cellular control systems in which the variables x^i typically represent the concentrations of certain molecules in the cell. Results on existence of periodic orbits have been given by Hastings *et al.* [19] and on stability in $\mathbf{R}^3$ by one of us [35]. See also R. A. Smith [38–40], who treated a different class of systems (but with some nontrivial overlap with those considered here).

Results which closely parallel our results here are given for the scalar reaction-diffusion equation

$$u_t = u_{\xi\xi} + f(\xi, u, u_\xi), \qquad u \in \mathbf{R}, \qquad \xi \in S^1 = \mathbf{R}/\mathbf{Z} \tag{0.8}$$

on the circle, by one of us with Fiedler [11], and for the scalar differential delay equation

$$\dot{x}(t) = -f(x(t), x(t-1)), \qquad x \in \mathbf{R} \tag{0.9}$$

jointly with Sell [29]. In the case of the delay equation (0.9) a monotonicity assumption $\partial f(x, y)/\partial y \neq 0$, for all (x, y), is needed; however, for the PDE (0.8) there is no monotonicity required of f. Indeed, a standard discretization of (0.9) with $x^i(t) = x(t - i/n)$, for $0 \leqslant i \leqslant n$, yields a monotone cyclic feedback system. A discretization of (0.8) based on $u^i(t) = u(t, i/n)$, for $1 \leqslant i \leqslant n$, yields a system

$$\dot{u}^i = g^i(u^{i-1}, u^i, u^{i+1}), \qquad 1 \leqslant i \leqslant n$$

with "nearest-neighbor" interactions, with g^i monotone in $u^{i\pm 1}$ (this monotonicity comes from the $u_{\xi\xi}$ term, and not from f). The behavior of such systems is not unlike that of the monotone cyclic feedback systems considered here.

The organization of this paper is as follows. In Section 1 a principal tool, an integer valued Lyapunov function N (due originally to Smillie

[34]) is developed. Section 2 is concerned with the Floquet theory of linear monotone cyclic feedback systems; the approach taken there is similar to one developed for an integral equation by Chow, Diekmann, and one of us [10]. Section 3 is devoted to the proof of our main result. Finally, in Section 4, the various applications outlined above are treated in depth.

1. AN INTEGER-VALUED LYAPUNOV FUNCTION

In this section we define a fundamental tool, an integer-valued Lyapunov function N, and develop some of its basic properties. The function N was first given by Smillie [34] and later used by Fusco and Oliva [13]. It is more or less the discrete analog of zero-crossing number of Matano [30] (discovered originally by Nickel [31]) for scalar reaction-diffusion equations.

We evaluate N along derivatives of solutions of (0.1) or along differences of two such solutions $x(t)$ and $\bar{x}(t)$:

$$N(\dot{x}(t)), \qquad N(x(t)-\bar{x}(t))$$

Indeed, this approach was used by Brunovský and Fiedler [9] with the Matano function in their study of connecting orbits in reaction–diffusion equations. Observe that if $x(t)$ and $\bar{x}(t)$ are two solutions of (0.1) in O, then $y(t)=\dot{x}(t)$ and $y(t)=x(t)-\bar{x}(t)$ satisfy a nonautonomous linear monotone cyclic feedback system

$$\dot{y}^i(t)=w^{i,i}(t)\, y^i(t)+w^{i,i-1}(t)\, y^{i-1}(t), \qquad 1\leqslant i\leqslant n \tag{1.1}$$

with

$$\delta^i w^{i,i-1}(t)>0 \qquad \text{and } w^{i,j} \text{ continuous}, \qquad j=i,\, i-1 \tag{1.2}$$

Indeed, for $y(t)=\dot{x}(t)$, (1.1) is just the variational equation about $x(t)$ with

$$w^{i,j}(t)=\partial f^i(x^i(t), x^{i-1}(t))/\partial x^j, \qquad j=i, \quad i-1,$$

while for $y(t)=x(t)-\bar{x}(t)$,

$$w^{i,j}(t)=\int_0^1 \partial f^i(u^i(s,t), u^{i-1}(s,t))/\partial x^j\, ds, \qquad j=i, \quad i-1,$$

where $u^i(s,t)=sx^i(t)+(1-s)\,\bar{x}^i(t)$.

Define the function N, taking values in $\{0, 1, 2,..., n\}$, by

$$N(y)=\operatorname{card}\{i \mid \delta^i y^i y^{i-1}<0\}$$

for those $y \in \mathbf{R}^n$ with each $y^i \neq 0$, $1 \leqslant i \leqslant n$. It is not difficult to see that the domain of definition of N can be extended (by continuity) to

$$\mathcal{N} = \{ y \in \mathbf{R}^n \mid y^i = 0 \quad \text{for some } i \text{ implies } \delta^{i+1}\delta^i y^{i+1} y^{i-1} < 0 \}$$

on which N is continuous. Observe that for those $y \in \mathbf{R}^n$ with each $y^i \neq 0$, $1 \leqslant i \leqslant n$,

$$(-1)^{N(y)} = \operatorname{sign} \prod_{i=1}^{n} \delta^i y^i y^{i-1} = \prod_{i=1}^{n} \delta^i = \Delta$$

It follows that N takes only odd values if $\Delta = -1$ and only even values if $\Delta = +1$. If $y \in \mathbf{R}^n - \mathcal{N}$, then $N(y)$ is undefined.

The following result justifies our definition of N. Except for (d), it is similar to a corresponding result of Smillie [34; see Proposition].

***Proposition* 1.1.** *Let $y(t)$ be a nontrivial solution of (1.1) where (1.2) holds. Then*

(a) $y(t) \in \mathcal{N}$ except at isolated values of t.

(b) $N(y(t))$ is locally constant where $y(t) \in \mathcal{N}$.

(c) If $y(t_0) \notin \mathcal{N}$, then $N(y(t_0+)) < N(y(t_0-))$.

(d) If $y(t) \in \mathcal{N}$, then $(y^i(t), y^{i-1}(t)) \neq (0, 0)$ and $(y^i(t), \dot{y}^i(t)) \neq (0, 0)$, $1 \leqslant i \leqslant n$.

Proof. We need only verify (a) and (c) since (b) and (d) are immediate from the definition of $\mathcal{N}$, continuity of $N(y(t))$, and (1.1), (1.2). Suppose that $y(t_0) \notin \mathcal{N}$ for some t_0. We assume without loss of generality that $t_0 = 0$. For $1 \leqslant i \leqslant n$, define $k(i) = k$, a nonnegative integer, if there exist $p^i \neq 0$ such that $y^i(t) = p^i t^k + o(t^k)$ as $t \to 0$, where $|o(t^k)/t^k| \to 0$ as $t \to 0$. In general, $k(i)$ may not be defined for some i. If $y^i(0) \neq 0$, then $k(i) = 0$ and $p^i = y^i(0)$. Hence $k(i)$ is defined for some i by our hypothesis that $y(0) \neq 0$. If $k(i)$ is defined we set $P^i = \operatorname{sign} p^i \in \{+1, -1\}$. Note that if $k(i)$ is defined, then $t = 0$ is an isolated zero of $y^i(t)$.

Let $Z = \{j : y^j(0) = 0\}$. Then Z is a nonempty proper subset of $\{1, 2, ..., n\}$. We can partition Z into a finite union of pairwise disjoint "intervals" $I_1, ..., I_l$, $l \geqslant 1$, satisfying that (a) each I_j consists of consecutive indices (mod n, e.g., $I_1 = \{n-1, n, 1, 2\}$) belonging to Z, and (b) if $I_j = \{i+1, i+2, ..., i+p\}$ (indices mod n), then i and $i+p+1$ do not belong to Z. Observe that it is conceivable that $l = 1$, i.e., there is only one such interval I as above with $i = i+p+1$ (mod n).

Consider a typical such interval I. Suppose first that $I = \{j\}$ is a singleton. There are two cases. If $\delta^{j+1}\delta^j P^{j+1} P^{j-1} = +1$, then $(d/dt)|_{t=0}\, \delta^j y^j y^{j-1} = \delta^j \dot{y}^j y^{j-1}|_{t=0} = \delta^j w^{j,j-1} (y^{j-1})^2 > 0$ and $(d/dt)|_{t=0}$ $\delta^{j+1} y^{j+1} y^j = \delta^{j+1} w^{j,j-1} y^{j+1} y^{j-1} > 0$. In particular, y^j has an isolated zero

$(k(j)=1)$ at $t=0$ and I contributes a decrease by two in N as t increases through zero. If $\delta^{j+1}\delta^{j}P^{j+1}P^{j-1}=-1$, then I contributes no change in N near $t=0$. Note that not all intervals I_j can be of this type since we assume $x(0)\notin \mathcal{N}$.

Now suppose $I=\{j+1, j+2,..., j+p\}$, $p\geqslant 2$. We show that $k(j+r)=r$, $0\leqslant r\leqslant p$ and $P^{j+r}=\delta^{j+r}P^{j+r-1}$, $1\leqslant r\leqslant p$. We require the following result; the simple proof is left to the reader.

Claim. *Let $y(t)$ be the solution of*

$$\dot{y}=A(t)\,y+g(t), \qquad y(0)=0$$

where $A(t)$ is a continuous $n\times n$ matrix function and $g(t)$ is a continuous n-vector function satisfying

$$g(t)=g_m t^m+o(t^m), \qquad t\to 0$$

where $g_m\in \mathbf{R}^n$ and m is a nonnegative integer. Then

$$y(t)=\frac{g_m}{m+1}\,t^{m+1}+o(t^{m+1})$$

Returning to the assertions above, note that $\dot{y}^{j+1}(0)=w^{j+1,j}y^{j}(0)$ so that $k(j+1)=1$ and $P^{j+1}=\operatorname{sign}(w^{j+1,j}(0)\,y^{j}(0))=\delta^{j+1}P^{j}$. Thus the assertions hold for $r=1$. Now $\dot{y}^{j+2}(t)=w^{j+2,j+2}y^{j+2}+w^{j+2,j+1}y^{j+1}$, $y^{j+2}(0)=0$, $w^{j+2,j+1}(t)\,y^{j+1}(t)=w^{j+2,j+1}(0)\,\dot{y}^{j+1}(0)\,t+o(t)$, so by the lemma above $k(j+2)=k(j+1)+1=2$ and

$$P^{j+2}=\operatorname{sign}(w^{j+2,j+1}(0)\,\dot{y}^{j+1})=\delta^{j+2}P^{j+1}$$

Continuing in this manner establishes the assertions above. It follows that $t=0$ is a simple zero of $y^{i}(t)$, $i\in I$.

For $q=1, 2,..., p$, $0<|t|$ and $|t|$ small

$$\begin{aligned}\operatorname{sign}(\delta^{j+q}y^{j+q}y^{j+q-1})&=\operatorname{sign}(\delta^{j+q}P^{j+q}P^{j+q-1}t^{2q-1})\\&=\delta^{j+q}P^{j+q}P^{j+q-1}\operatorname{sign}t^{2q-1}\\&=(\delta^{j+q}P^{j+q-1})^2\operatorname{sign}t^{2q-1}\\&=\operatorname{sign}t^{2q-1}\end{aligned}$$

Furthermore,

$$\operatorname{sign}(\delta^{j+p+1}y^{j+p+1}y^{j+p})=\delta^{j+p+1}P^{j+p+1}P^{j+p}\operatorname{sign}t^{p}$$

for $|t|$ small and positive.

Hence as t increases through zero (t sufficiently near zero) the interval I contributes to a change in N of

$$\Delta N = \begin{cases} -p & p \text{ even} \\ -(p+1) & p \text{ odd and } \delta^{j+p+1} p^{j+p+1} p^{j+p} > 0 \\ -(p-1) & p \text{ odd and } \delta^{j+p+1} p^{j+p+1} p^{j+p} < 0 \end{cases}$$

Observe that in each case, the change is a negative even integer.

In summary, we have decomposed Z into a disjoint union of $l \geqslant 1$ intervals. Except in the case of one special type of singleton interval, we found that for each of these intervals, y^j has a simple zero at $t=0$ for each j in the interval and that each such interval contributed a decrease in N by an even positive integer as t increases through zero in a small neighborhood of zero. Further, we showed that this special type of singleton interval contributed no change in N but that not every interval could be of this type. From these considerations, (a) and (c) of Proposition 1.1 follow. ∎

The following consequences of Proposition 1.1 are crucial to our analysis of (0.1). Let $x(t)$ and $\bar{x}(t)$ be two distinct solutions of (0.1) in O which exist for $t \geqslant 0$. Then Proposition 1.1 implies that $N(x(t)-\bar{x}(t))$ is constant except at a *finite* number of points $t_1, t_2, \ldots, t_p$, $(p \leqslant [n/2])$ at which $N(x(t)-\bar{x}(t))$ is not defined. As t increases through t_j, $1 \leqslant j \leqslant p$, $N(x(t)-\bar{x}(t))$ decreases by a positive multiple of two. For each i, $1 \leqslant i \leqslant n$, and for t belonging to one of the intervals $(t_j, t_{j+1})(t_p, +\infty)$, property (d) implies the projections of $x(t)$ and $\bar{x}(t)$ into the (x^i, x^{i-1}) plane do not meet: $(x^i(t), x^{i-1}(t)) \neq (\bar{x}^i(t), \bar{x}^{i-1}(t))$. (This does not prove the two curves so described are disjoint in the plane but does raise the possibility, at least for large t.) The same is true for the projections into the $(x^i, \dot{x}^i)$-plane; equivalently, the zeros of $x^i(t)-\bar{x}^i(t)$ are simple in these intervals. The above observations suggest the possibility of using phase plane analysis to determine qualitative properties of solutions of (0.1). This expectation is realized in Section 3.

2. LINEAR SYSTEMS

We consider the n-dimensional linear system

$$\dot{x} = W(t)\, x, \qquad W(t+\tau) \equiv W(t), \tag{2.1}$$

of period $\tau > 0$ (not necessarily the least period) and assume this is a monotone cyclic feedback system:

$$w^{ij}(t) \equiv 0 \qquad \text{unless } j = i \text{ or } i-1,$$

$$\delta^i w^{i,i-1}(t) > 0 \qquad \text{for all } t, \text{ and } w^{i,j} \text{ continuous, } j = i, i-1$$

Let $X(t)$ denote the fundamental matrix solution of (2.1) with $X(0) = I$ and define, for a given $\alpha \in \mathbf{C} - \{0\}$, the complex eigenspaces

$$E_\alpha = \ker(X(\tau) - \alpha I) \subset \mathbf{C}^n$$

$$G_\alpha = \text{gen}\ker(X(\tau) - \alpha I) \subset \mathbf{C}^n$$

[Here gen ker $A = \ker A^m$, for large m, is the generalized kernel of a matrix. The system (2.1) is assumed real, even though here we take complex eigenspaces.] Given $\sigma > 0$ define

$$\mathscr{E}_\sigma = \operatorname{Re} \bigoplus_{|\alpha| = \sigma} E_\alpha$$

$$\mathscr{G}_\sigma = \operatorname{Re} \bigoplus_{|\alpha| = \sigma} G_\alpha$$

the real parts of the spans.

Lemma 2.1. *Given $\sigma > 0$ there exists an integer k, such that for each initial condition $x_0 \in \mathscr{E}_\sigma - \{0\}$, the solution $x(t)$ of (2.1) satisfies $N(x(t)) = k$ for all t. Furthermore, all zeros of $x^i(t)$, for each i, are simple.*

Proof. Letting $\mu \in \mathbf{R}$ satisfy $e^{\mu\tau} = \sigma$, we see from Floquet theory that $x(t) = e^{\mu t} q(t)$ where $q(t)$ is quasi-periodic. Fix $t_0 \in \mathbf{R}$ so that $q(t_0) \in \mathscr{N}$; then there exists $t_1 < t_0 < t_2$, with $|t_1|$ and $|t_2|$ arbitrarily large, so that $q(t_1)$ and $q(t_2)$ are in the same component of $\mathscr{N}$ as $q(t_0)$. As N is constant on each component of $\mathscr{N}$, we have for $j = 1, 2$

$$N(x(t_j)) = N(q(t_j)) = N(q(t_0))$$

hence $N(x(t_1)) = N(x(t_2))$. The monotonicity of $N(x(t))$ in t thus implies that this quantity is a constant $k(x_0)$ independent of t.

The fact that $k(x_0)$ is a well-defined integer for $x_0 \in \mathscr{E}_\sigma - \{0\}$, and is locally constant, implies that $k(x_0) \equiv k$ is independent of such x_0. Finally, the simplicity of the zeros of $x^i(t)$ follows from Proposition 1.1. ∎

Lemma 2.2. *The statement of Lemma 2.1 holds, with $\mathscr{G}_\sigma$ replacing $\mathscr{E}_\sigma$.*

Proof. If $y_0 \in \mathscr{G}_\sigma - \{0\}$, then $y(t) = t^a e^{\mu t} q(t) + 0(t^{a-1} e^{\mu t})$ as $t \to \pm\infty$, where $x(t) = e^{\mu t} q(t)$ is as above [that is, $x(0) = x_0 \in \mathscr{E}_\sigma - \{0\}$]. With t_1 and t_2 as above, one has for $j = 1, 2$ that $t_j^{-a} e^{-\mu t_j} y(t_j)$ is arbitrarily close to $q(t_j)$ and, hence, to $q(t_0)$. Thus

$$N(y(t_j)) = N(t_j^{-a} e^{-\mu t_j} y(t_j)) = N(q(t_0)) = k$$

Thus, the local constancy of N, and monotonicity of N, yields the first result. The simplicity of zeros again follows from Proposition 1.1. ∎

***Lemma* 2.3.** *If $\sigma < \tilde{\sigma}$ are norms $\sigma = |\alpha|$ and $\tilde{\sigma} = |\tilde{\alpha}|$ of characteristic multipliers α and $\tilde{\alpha}$, then one has $k \geqslant \tilde{k}$ for the values of N on the spaces $\mathscr{G}_\sigma$ and $\mathscr{G}_{\tilde{\sigma}}$.*

Proof. Let $x_0 \in \mathscr{G}_\sigma - \{0\}$, $\tilde{x}_0 \in \mathscr{G}_{\tilde{\sigma}} - \{0\}$, let $x(t)$ and $\tilde{x}(t)$ denote the solutions through these points, and set $y(t) = x(t) + \tilde{x}(t)$. One has $x(t) = e^{\mu t} t^a q(t)$ and $\tilde{x}(t) = e^{\tilde{\mu} t} t^{\tilde{a}} \tilde{q}(t)$ for $\mu < \tilde{\mu}$ and quasiperiodic $q(t)$ and $\tilde{q}(t)$. Observing that $e^{-\mu t} t^{-a} y(t) - q(t) \to 0$ as $t \to -\infty$, one has, as in the lemma above, that

$$N(y(t)) = N(e^{-\mu t} t^{-a} y(t)) = N(q(t)) = N(x(t)) = k$$

for t arbitrarily near $-\infty$. Similarly, one has $N(y(t)) = \tilde{k}$ for t near ∞. Thus, $k \geqslant \tilde{k}$ by the monotonicity of N. ∎

***Lemma* 2.4.** *If $S = \{\sigma\}$ is a set of positive numbers, which are all norms $\sigma = |\alpha|$ of characteristic multipliers, and if the value $N = k$ on $\mathscr{G}_\sigma$ is independent of $\sigma \in S$, then $N(x(t)) \equiv k$ for any nontrivial solution with initial condition $x_0 \in \operatorname{span}_{\sigma \in S} \mathscr{G}_\sigma$.*

Proof. Write $x(t) = \sum_{\sigma \in S} x_\sigma(t)$ as a finite sum of solutions with initial conditions in each $\mathscr{G}_\sigma$. Then argue as in the proof of Lemma 2.3 to show that $N(x(t)) = k$ both as $t \to -\infty$ and as $t \to \infty$. Thus, $N(x(t))$ is the constant k. ∎

***Lemma* 2.5.** *If S is as in Lemma 2.4, then*

$$\dim \operatorname*{span}_{\sigma \in S} \mathscr{G}_\sigma \leqslant 2$$

In particular, for any $\sigma > 0$ one has

$$\dim \mathscr{G}_\sigma \leqslant 2$$

Proof. Suppose the space $\operatorname{span}_{\sigma \in S} \mathscr{G}_\sigma$ in question has dimension three or more. Then there exists a nontrivial solution $x(t)$ with initial condition x_0 in that space, such that the first coordinate $x^1(t)$ has a multiple zero at $t = 0$:

$$x^1(0) = \dot{x}^1(0) = 0$$

Such a solution is easily found by taking a nontrivial linear combination of three linearly independent solutions. Now $N(x(t)) \equiv k$ is constant in t, by Lemma 2.4; but this contradicts Proposition 1.1. ∎

Index the characteristic multipliers $\{\alpha_k\}_{k=1}^n$, and the quantities $\sigma_k = |\alpha_k|$, so that

$$\sigma_1 \geqslant \sigma_2 \geqslant \cdots \geqslant \sigma_n$$

and assume for definiteness that $\Delta = -1$. In case $n = 2b$ is even, it is clear from the fact that N can only take on the $n/2$ values 1, 3, 5,..., $2b-1$, and from Lemmas 2.2–2.5, that

$$\sigma_1 \geqslant \sigma_2 > \sigma_3 \geqslant \sigma_4 > \cdots > \sigma_{n-1} \geqslant \sigma_n \tag{2.2}$$

(that is, the inequality $\sigma_{2h} > \sigma_{2h+1}$ is strict) and that

$$N = 2h - 1 \text{ on } \mathscr{G}_{\sigma_{2h-1}} + \mathscr{G}_{\sigma_{2h}} \qquad \text{for} \quad h = 1, 2,..., b. \tag{2.3}$$

If, on the other hand, n is odd, then the situation is not as clear. We show below, however, that

$$\sigma_1 \geqslant \sigma_2 > \sigma_3 \geqslant \sigma_4 > \cdots > \sigma_{n-2} \geqslant \sigma_{n-1} > \sigma_n \tag{2.4}$$

and that in addition to (2.3), with $n = 2b + 1$, we have

$$N = 2h - 1 \text{ on } \mathscr{G}_{\sigma_{2h-1}} \qquad \text{for } h = b + 1, \tag{2.5}$$

that is, $N = n$ on $\mathscr{G}_{\sigma_n}$. Also, products of certain pairs of multipliers are shown to be positive.

Theorem 2.6. *Assume first that $\Delta = -1$. If the dimension $n = 2b$ is even, then the norms $\sigma = |\alpha|$ of the characteristic multipliers satisfy (2.2), and N takes the values (2.3) on the spaces $\mathscr{G}_{\sigma_{2h-1}} + \mathscr{G}_{\sigma_{2h}}$, each of which is two-dimensional. Furthermore,*

$$\alpha_{2h-1}\alpha_{2h} > 0 \qquad \textit{for } h = 1, 2,..., b \tag{2.6}$$

If $n = 2b + 1$ is odd, then one has (2.3), (2.4), and also (2.5), the spaces $\mathscr{G}_{\sigma_{2h-1}} + \mathscr{G}_{\sigma_{2h}}$ and $\mathscr{G}_{\sigma_{2b+1}}$ being two- and one-dimensional, respectively. One also has (2.6) and, in addition,

$$\alpha_{2h-1} > 0 \qquad \textit{for } h = b + 1, \tag{2.7}$$

that is, $\alpha_n > 0$.

Now assume that $\Delta = +1$. If $n = 2b - 1$ is odd, then

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

and

$$N = 0 \text{ on } \mathcal{G}_{\sigma_1} \tag{2.8}$$

$$N = 2h \text{ on } \mathcal{G}_{\sigma_{2h}} + \mathcal{G}_{\sigma_{2h+1}} \qquad \text{for } h = 1, 2,..., b-1 \tag{2.9}$$

where $\mathcal{G}_{\sigma_1}$ *is one-dimensional and* $\mathcal{G}_{\sigma_{2h}} + \mathcal{G}_{\sigma_{2h+1}}$ *is two-dimensional.*
Furthermore,

$$\alpha_1 > 0, \tag{2.10}$$

$$\alpha_{2h}\alpha_{2h+1} > 0 \qquad \text{for } h = 1, 2,..., b-1 \tag{2.11}$$

both hold. When $n = 2b$ *is even, then*

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

and (2.8)–(2.11) *all hold. In addition*

$$N = 2h \text{ on } \mathcal{G}_{\sigma_{2h}}$$

and

$$\alpha_{2h} > 0, \qquad \text{both with } h = b \text{ (that is, } 2h = n),$$

and $\mathcal{G}_{\sigma_{2h}}$ *is one-dimensional.*

Proof. For simplicity, we consider only the case $\Delta = -1$, as the proof for $\Delta = +1$ is analogous. As noted above, Lemmas 2.2–2.5 force (2.2) and (2.3) if n is even. Similarly, one sees that if $n = 2b + 1$ is odd, then there is a distinguished odd integer $2c + 1 \in \{1, 3, 5,..., n\}$ such that

$$\begin{aligned} &\sigma_1 \geqslant \sigma_2 > \sigma_3 \geqslant \sigma_4 > \cdots \\ &\quad \cdots > \sigma_{2c-1} \geqslant \sigma_{2c} > \sigma_{2c+1} > \sigma_{2c+2} \geqslant \sigma_{2c+3} > \cdots \\ &\qquad \cdots > \sigma_{2b-2} \geqslant \sigma_{2b-1} > \sigma_{2b} \geqslant \sigma_{2b+1} \end{aligned}$$

and such that

$$N = \begin{cases} 2h - 1 \text{ on } \mathcal{G}_{\sigma_{2h-1}} + \mathcal{G}_{\sigma_{2h}} & \text{for } h = 1, 2,..., c \\ 2c + 1 \text{ on } \mathcal{G}_{\sigma_{2c+1}} & \\ 2h + 1 \text{ on } \mathcal{G}_{\sigma_{2h}} + \mathcal{G}_{\sigma_{2h+1}} & \text{for } h = c+1, c+2,..., b \end{cases}$$

We wish to show that $c = b$, that is, $2c + 1 = n$ as in (2.4). From this (2.4) and (2.5) immediately follow, again by the lemmas above.

To prove that $c = b$, we consider a homotopy

$$W_\rho(t) = \rho W(t) + (1 - \rho)\, W_0$$

of the coefficient matrix such that (2.1) is a monotone cyclic feedback system throughout $0 \leqslant \rho \leqslant 1$. (At $\rho = 0$ we consider the autonomous equation $\dot{x} = W_0 x$ as being τ-periodic.) To be specific we choose $W_0^{i,i-1} = \delta^i$ for all i, and $W_0^{ij} = 0$ for $j \neq i-1$ as the entries of W_0. This corresponds to the nth-order scalar equation $d^n x^1/dt^n = -x^1$ and one easily sees that $c = b$ for this system. Now the quantities $\sigma_k = \sigma_k(\rho)$ vary continuously in ρ, and so the values of N on each $\mathscr{G}_{\sigma_k}$ are independent of ρ. Thus $c(\rho) \equiv b$ is constant throughout the homotopy, establishing (2.4) and (2.5).

To prove (2.6) and (2.7) we observe that $\mathscr{G}_{\sigma_{2h-1}} + \mathscr{G}_{\sigma_{2h}}$ (and $\mathscr{G}_{\sigma_{2b+1}}$ for n odd) are spectral subspaces of $X(\tau)$ and the determinants of $X(\tau)$ on these subspaces are given by the quantities in (2.6) and (2.7). Throughout the homotopy above, these subspaces and determinants vary continuously in ρ, and one verifies positivity of the determinants at $\rho = 0$. As $X(\tau)$ is nonsingular, positivity is maintained throughout the homotopy. ∎

Remark 2.1. If $\Delta = +1$, then each nonconstant periodic solution of a monotone cyclic feedback system (0.1) is unstable, i.e., $\sigma_1 > 1$. See Lemma 1.2 in Ref. 35.

3. MONOTONE SYSTEMS

Let us now consider a nonlinear monotone cyclic feedback system

$$\dot{x}^i = f^i(x^i, x^{i-1}), \qquad i = 1, 2,..., n \ (\mathrm{mod}\ n), \tag{3.1}$$

that is, f is C^1 and satisfies (0.2) everywhere.

Proposition 3.1. *Let $p(t)$ be a periodic solution of (3.1) of least period $\tau > 0$. Then for each i the maps*

$$t \to (p^i(t), \dot{p}^i(t)) \qquad \text{and } t \to (p^i(t), p^{i-1}(t)) \tag{3.2}$$

are embeddings of the circle $S^1 = \mathbf{R}/\tau\mathbf{Z}$ into $\mathbf{R}^2$; that is, they are one-to-one on $[0, \tau)$ and have nonzero derivative throughout $[0, \tau)$. In particular, if $\gamma = \{p(t): t \in \mathbf{R}\}$ is the periodic orbit of (3.1), then $\gamma^i \equiv \Pi^i \gamma$ is a Jordan curve in $\mathbf{R}^2$ for each i.

Moreover, there is an integer k_0 such that for each $\theta \in (0, \tau)$

$$N(p(t+\theta) - p(t)) = N(\dot{p}(t)) = k_0 \tag{3.3}$$

holds for all t.

Proof. Fix $\theta \in (0, \tau)$, let $z(t) = p(t+\theta) - p(t)$, and observe that $z(t)$ is a nontrivial solution of the linear monotone cyclic feedback system (1.1), with coefficients

$$w^{ij}(t) = \int_0^1 \frac{\partial f^i(u^i(s,t), u^{i-1}(s,t))}{\partial x^j}\, ds \tag{3.4}$$

where

$$u^i(s,t) = sp^i(t+\theta) + (1-s)\, p^i(t)$$

As $z(t)$ is periodic, Proposition 1.1 implies that $N(z(t)) \equiv k$ is constant in t (with k possibly depending on θ, however). Proposition 1.1 also implies that all zeros of each $z^i(t)$ are simple: for all $t \in \mathbf{R}$

$$(z^i(t), \dot{z}^i(t)) \neq (0,0) \qquad \text{equivalently, } (z^i(t), z^{i-1}(t)) \neq (0,0). \tag{3.5}$$

The conditions (3.5) and the fact that $\theta \in (0, \tau)$ is arbitrary are easily seen to imply that the maps (3.2) are one-to-one on $[0, \tau)$.

To prove the nonvanishing

$$(\dot{p}(t), \ddot{p}(t)) \neq (0,0) \qquad \text{and} \qquad (\dot{p}^i(t), \dot{p}^{i-1}(t)) \neq (0,0)$$

of the derivatives, one simply observes that $q(t) = \dot{p}(t)$ satisfies the linear variational equation $\dot{q} = Df(x(t))\, q$. As this equation is a monotone cyclic feedback system, $N(q(t)) \equiv k_0$ is constant and one argues as above. In order to verify (3.3), observe that for $\theta > 0$ sufficiently small $\theta^{-1}[p(t+\theta) - p(t)]$ is uniformly near $\dot{p}(t)$ and so belongs to $\mathcal{N}$ and $N(p(t+\theta) - p(t)) = N(\theta^{-1}[p(t+\theta) - p(t)]) = N(\dot{p}(t)) = k_0$. That (3.3) holds for all values of $\theta \in (0, \tau)$ follows from the local constancy of N on $\mathcal{N}$. ∎

Proposition 3.2. *Let γ_j be an equilibrium or periodic orbit of (3.1), for $j = 1, 2$. If γ_1 and γ_2 are distinct orbits, then their projections $\gamma_1^i = \Pi^i \gamma_1$, $\gamma_2^i = \Pi^i \gamma_2$ do not intersect in $\mathbf{R}^2$, for each i. If γ_1 and γ_2 are distinct nonconstant periodic orbits such that for some i, γ_1^i belongs to the interior component of $\mathbf{R}^2 - \gamma_2^i$, then γ_1^i belongs to the interior component of $\mathbf{R}^2 - \gamma_2^i$ for every i.*

Proof. Let $p_j(t)$ be the solution of (3.1) which parametrizes γ_j, $j = 1, 2$. Then for every $\theta \in \mathbf{R}$, $z(t) = p_1(t+\theta) - p_2(t)$ is a nontrivial quasiperiodic solution of a linear monotone cyclic feedback system (1.1). Arguing exactly as in Lemma 2.1, we obtain an integer $k(\theta)$ such that

$$N(p_1(t+\theta) - p_2(t)) = k(\theta)$$

for all $t \in \mathbf{R}$. One can show that $k(\theta)$ is independent of θ, although this fact is not essential for our conclusions. As in Proposition 3.1, we obtain (3.5) and this implies that γ_1^i and γ_2^i do not meet in $\mathbf{R}^2$, for each i.

Now suppose that γ_1 and γ_2 are distinct nonconstant periodic orbits and $p_j(t)$, $j=1, 2$, parametrize γ_1 and γ_2, respectively. From above, the projections γ_1^i and γ_2^i do not meet, and moreover, the images of the maps $t \mapsto (p_j^i(t), \dot{p}_j^i(t))$, $j=1, 2$, for fixed i, do not meet. The latter implies that for each i either Range p_1^i and Range p_2^i do not intersect or one is contained in the interior of the other. Now suppose that γ_1^i belongs to the interior of γ_2^i for some i. Then Range p_1^{i-1} is contained in the interior of Range p_2^{i-1}. Let $c = \max p_1^{i-1} = p_1^{i-1}(0)$. Then $\dot{p}_1^{i-1}(0) = f^{i-1}(c, p_1^{i-2}(0)) = 0$ and since c belongs to the interior of the range of p_2^{i-1}, there are two distinct values of t at which p_2^{i-1} attains the value c in the half-open interval from zero to the period of p_2, say $p_2^{i-1}(t_+) = p_2^{i-1}(t_-) = c$, and $\dot{p}_2^{i-1}(t_+)\, \dot{p}_2^{i-1}(t_-) = f^{i-1}(c, p_2^{i-2}(t_+))\, f^{i-1}(c, p_2^{i-2}(t_-)) < 0$. It follows from the monotonicity of $f^{i-1}(c, \cdot)$ that $p_1^{i-2}(0)$ lies between $p_2^{i-2}(t_+)$ and $p_2^{i-2}(t_-)$. This in turn implies that $(p_2^{i-1}(t_+), p_2^{i-2}(t_+))$ and $(p_2^{i-1}(t_-), p_2^{i-2}(t_-))$ lie in the exterior component of $\mathbf{R}^2 - \gamma_1^{i-1}$ and hence γ_1^{i-1} belongs to the interior component of γ_2^{i-1}. Iterating this argument completes the proof. ∎

If γ_1 and γ_2 are distinct nonconstant periodic orbits of (3.1) such that γ_1^i is contained in the interior component of $\mathbf{R}^2 - \gamma_2^i$ for every i, then we write $\gamma_1 < \gamma_2$. We write $\gamma_1 \leqslant \gamma_2$ if either $\gamma_1 = \gamma_2$ or $\gamma_1 < \gamma_2$. The relation $\leqslant$ is a partial order on the set of nonconstant periodic orbits.

Remark 3.1. It is interesting to observe that if γ^i is the image of the second map in (3.2), then there exists an equilibrium point x_* of (3.1) such that (x_*^i, x_*^{i-1}) belongs to the interior component of $\mathbf{R}^2 - \gamma^i$ for each i, $1 \leqslant i \leqslant n$. Note that if $a^i = \min\{p^i(t): t \in \mathbf{R}\}$ and b^i is the corresponding maximum, $1 \leqslant i \leqslant n$, then the fact that $(p_i(t), \dot{p}_i(t))$ describes a Jordan curve implies that each value $\bar{x}_i \in (a_i, b_i)$ is assumed exactly twice by $p_i(t)$ in a half-open interval $[0, \tau)$, where $\tau =$ period p. This implies that for each $\bar{x}^i$ in (a^i, b^i), there are exactly two points of intersection of γ^i with the line $x^i = \bar{x}^i$. For $x^i = a^i$ or b^i there is precisely one point of intersection. The monotonicity of f^i, the intermediate value theorem, and the implicit function theorem together imply the existence of a smooth map $g^i\colon [a^i, b^i] \to [a^{i-1}, b^{i-1}]$, the graph of which lies in the interior component of $\mathbf{R}^2 - \gamma^i$, except for the points $(a^i, g^i(a^i))$ and $(b^i, g^i(b^i))$ which lie on γ^i, and such that $f^i(x^i, g^i(x^i)) \equiv 0$ on $[a^i, b^i]$. The map $g \equiv g_2 \circ g_3 \circ \cdots \circ g_n \circ g_1 : [a^1, b^1] \to [a_1, b_1]$ has a fixed point x_*^1 and x_*, defined by $x_*^{i-1} = g^i(x_*^i)$, $1 \leqslant i \leqslant n$, $i \neq 2$, defines an equilibrium point with the above-mentioned properties.

Theorem 3.3. *Let γ be a nonconstant periodic orbit of (3.1) of minimal period τ. Then for any neighborhood N of τ in $\mathbf{R}$ and any neighborhood U of γ in O, there exists a neighborhood W of γ, $W \subset U$, such that if $\tilde{\gamma}$ is a periodic orbit of (3.1) with $\tilde{\gamma} \cap W \neq \phi$, then $\tilde{\gamma} \subset U$ and Period $(\tilde{\gamma}) \in N$.*

Proof. We make use of the observations made in Remark 3.1. Let $\gamma = \{p(t): t \in \mathbf{R}\}$ where $p(t)$ is a τ-periodic solution of (3.1). Fix i and assume without loss of generality that $p^i(0) = c^i \in (a^i, b^i)$ and $\dot{p}^i(0) > 0$ (a^i and b^i are defined in Remark 3.1). Then the intersection of a small open ball about $p(0)$ with the hyperplane $x^i = c^i$ provides an $n-1$ cell, I_i, transverse to the flow ($f^i > 0$ on I_i). In a neighborhood V of $p(0)$ in I_i there is defined a smooth first-return-time map $T: V \to (0, \infty)$ satisfying $T(p(0)) = \tau$ and, for $x(0) \in V$, $x(t) \notin I_i$ for $0 < t < T(x(0))$ and $x(T(x(0))) \in I_i$. Since T is continuous on V, $V' = T^{-1}(N)$ is a neighborhood of $p(0)$. Choose an open path ring W enclosing γ (see Ref. 17, p. 45) such that $W \subset U$ and $W \cap I_i \subset V'$.

Now suppose that $\tilde{\gamma}$ is a nonconstant periodic orbit such that $\tilde{\gamma} \cap W$ is nonempty. By properties of a path ring, we may suppose that there is a point of $\tilde{\gamma} \cap W$ belonging to V'. Let $q(0)$ denote such a point and $q(t)$ be the periodic solution of (3.1) with minimal period $\tilde{\tau}$. Since $q(0) \in V'$, $q(t)$ first meets I_i for $t > 0$ at $t = T(q(0))$. But by the arguments of Remark 3.1, $q(t)$ meets I_i at most once per period, i.e., $q^i(t) = c^i$ and $\dot{q}^i(t) > 0$ for at most one $t \in [0, \tilde{\tau})$. It follows that $\tilde{\tau} = T(q(0))$ and so $\tilde{\tau} \in N$ since $q(0) \in V'$. Moreover, since $q(t) \in W$ for $0 \leqslant t < T(q(0)) = \tilde{\tau}$, we find that $\tilde{\gamma} \subset W \subset U$. ∎

Corollary 3.4. *Let γ be a nontrivial periodic orbit of (3.1) and let B be an arbitrary compact subset of O. Let $\Pi^i: \mathbf{R}^n \to \mathbf{R}^2$ be the projection, $\Pi^i x = (x^i, x^{i-1})$. Then either*

(a) there exists a neighborhood V of $\Pi^i \gamma$ in $\mathbf{R}^2$ such that $\Pi^i \tilde{\gamma} \cap (V - \Pi^i \gamma) = \phi$ for every periodic orbit $\tilde{\gamma} \subset B$, or

(b) there exists a sequence $\{\gamma_m\}$ of nontrivial periodic orbits, $\gamma_m \neq \gamma$, $\gamma_m \subset B$, $m \geqslant 1$, and points $z_m \in \Pi^i \gamma_m$, $w_m \in \Pi^i \gamma$ such that $z_m - w_m \to 0$ as $m \to \infty$. In this case, Period $\gamma_m \to$ Period γ and $\gamma_m \to \gamma$ as $m \to \infty$, the latter in the Hausdorff metric.

Proof. Suppose that (a) does not hold. Then there exists a sequence $\{\gamma_m\}$ of nontrivial periodic orbits $\gamma \neq \gamma_m \subset B$, satisfying the following. Let $\gamma = \{p(t): t \in \mathbf{R}\}$ and $\gamma_m = \{p_m(t): t \in \mathbf{R}\}$ where p, p_m are periodic solutions of (3.1). Without loss of generality, we may assume that $\Pi^i p_m(0) \to \Pi^i p(0)$ and $p_m(0) \to z$ as $m \to \infty$. Let $z(t)$ be the solution of (3.1) satisfying $z(0) = z$. Since $\Pi^i z(0) = \Pi^i p(0)$, it follows that $p(0) - z(0) \notin \mathcal{N}$ and, by

Proposition 1.1, either $p(t) \equiv z(t)$ or $N(p(-t)-z(-t)) < N(p(t)-z(t))$ for all sufficiently small positive t. If the latter is the case, then since $\mathscr{N}$ is open and N is continuous, we have

$$N(p(-t)-p_m(-t)) < N(p(t)-p_m(t))$$

for all large m and some fixed small positive t. But Proposition 1.1 and the fact that $p(t)-p_m(t)$ is almost periodic in t imply that $p(t)-p_m(t) \in \mathscr{N}$ for all t and that $N(p(t)-p_m(t))$ is identically constant (depending on m) for each $m \geqslant 1$. This contradiction implies that $p(t) \equiv z(t)$ and that $p_m(0) \to p(0)$ as $m \to \infty$. The conclusion (b) now follows from Theorem 3.3. ▮

Now consider a solution $x(t)$, through $x(0)=x_0$, whose forward orbit is bounded, with closure $\overline{\gamma^+(x_0)} \subset O$. We keep this solution fixed for the remainder of this section.

Lemma 3.5. *If the orbit through $y_0 \in \omega(x_0)$ is neither an equilibrium nor a periodic solution, then for each i the maps*

$$t \to (y^i(t), \dot{y}^i(t)) \qquad \textit{and} \qquad t \to (y^i(t), y^{i-1}(t))$$

are immersions of $\mathbf{R}$ into $\mathbf{R}^2$, that is, are one-to-one with nonzero derivative for all $t \in \mathbf{R}$.

Proof. Let $t_m \to \infty$ be such that $x(t_m) \to y_0$. Fix $\theta \in \mathbf{R}$, $\theta \neq 0$, and set $z_m(t) = x(t+t_m+\theta) - x(t+t_m)$ and $z(t) = y(t+\theta) - y(t)$. Then $z_m(t)$ satisfies the monotone cyclic feedback system (1.1) but with coefficients

$$w_m^{ij}(t) = \int_0^1 \frac{\partial f^i}{\partial x^j}(u_m^i(s, t), u_m^{i-1}(s, t))\, ds$$

where

$$u_m^i(s, t) = s x^i(t+t_m+\theta) + (1-s)\, x^i(t+t_m),$$

and $z(t)$ satisfies the limiting system (1.1), the coefficients (3.4) with $y(t)$ replacing $p(t)$. The quantity

$$k = \lim_{m \to \infty} N(z_m(t)) = \lim_{s \to \infty} N(x(s+\theta) - x(s))$$

is therefore independent of t; thus, as $z_m(t) \to z(t)$ one has $N(z(t)) = k$ whenever $z(t) \in \mathscr{N}$ and hence for all $t \in \mathbf{R}$ by Proposition 1.1. With the constancy of $N(z(t))$ established, the remainder of the proof is as that of Proposition 3.1. ▮

Lemma 3.6. *If $y_0 \in \omega(x_0)$, then $\omega(y_0)$ contains at least one equilibrium or periodic orbit. The same is true of $\alpha(y_0)$. Thus $\omega(x_0)$ contains at least one equilibrium or periodic orbit.*

Proof. Fix $y_0 \in \omega(x_0)$ and let $y(t)$ denote the solution through this point. We prove the result for $\omega(y_0)$, the proof for $\alpha(y_0)$ being similar. Assume therefore that the result is false, that is, $\omega(y_0)$ contains neither an equilibrium nor a periodic orbit. If for some i the limit $y^i(t) \to y^i_\infty$ exists as $t \to \infty$, then equicontinuity of $\dot{y}^i(t)$ (from the ODE) implies that $\dot{y}^i(t) \to 0$. Monotonicity of f^i in y^{i-1} thus forces the limit $y^{i-1}(t) \to y^{i-1}_\infty$ to exist, for some y^{i-1}_∞, and one sees therefore that $\lim_{t\to\infty} y(t) = y_\infty$ exists. But then $y_\infty \in \omega(y_0) \subset \omega(x_0)$ is an equilibrium in $\omega(x_0)$, a contradiction.

Therefore, we have for each i that $y^i(t)$ does not approach a limit:

$$\liminf_{t\to\infty} y^i(t) < \limsup_{t\to\infty} y^i(t)$$

By Lemma (3.5) for any i all zeros of $\dot{y}^i(t)$ are simple, and we know there are infinitely many of them. Fix i, and denote the zeros of $\dot{y}^i(t)$ by $\{t_m\}$, ordered $t_m < t_{m+1}$. Without loss $\dot{y}^i(t) \geqslant 0$ in $[t_{2m-1}, t_{2m}]$ and $\dot{y}^i(t) \leqslant 0$ in $[t_{2m}, t_{2m+1}]$, with strict inequalities in the interiors of these intervals. Set $\eta_m = y^i(t_m)$; then $\eta_{2m\pm1} < \eta_{2m}$ holds. With $I_m = [\eta_{2m-1}, \eta_{2m}]$ and $J_m = [\eta_{2m+1}, \eta_{2m}]$, we have continuous functions $\phi_m: I_m \to [0, \infty)$ and $\psi_m: J_m \to (-\infty, 0]$ defined by setting

$$\begin{aligned} \dot{y}^i(t) &= \phi_m(y^i(t)), && t \in [t_{2m-1}, t_{2m}] \\ \dot{y}^i(t) &= \psi_m(y^i(t)), && t \in [t_{2m}, t_{2m+1}] \end{aligned} \tag{3.6}$$

The functions ϕ_m and ψ_m vanish only at the end points of their domains I_m, J_m, and are C^1 in the interiors of these intervals. Differentiating (3.6) with respect to t and using the boundedness of $\ddot{y}^i(t)$ as $t \to \infty$ (from the ODE) yields estimates

$$|\dot{\phi}_m(\eta)| \leqslant \frac{K}{|\phi_m(\eta)|}, \qquad |\dot{\psi}_m(\eta)| \leqslant \frac{K}{|\psi_m(\eta)|} \tag{3.7}$$

for all η in the interiors of I_m and J_m, with $K > 0$ independent of m.

We now exploit the fact that the image $(y^i(t), \dot{y}^i(t))$ in the $(y^i, \dot{y}^i)$-plane is a one-to-one parameterization in t. This fact alone implies that the intervals I_m and J_m, and the functions ϕ_m and ψ_m are monotone in m. Indeed, either the relations

$$\begin{aligned} &I_m \supseteq J_m \supseteq I_{m+1} \\ &\phi_m(\eta) > \phi_{m+1}(\eta) && \text{in } I_m \cap I_{m+1} \\ &\psi_m(\eta) < \psi_{m+1}(\eta) && \text{in } J_m \cap J_{m+1} \end{aligned} \tag{3.8}$$

hold for all m, or else these relations with the inclusions and inequalities reversed hold for all m. The proof of this fact utilizes the Jordan curve theorem in a fashion similar to that in the proof of the Poincaré–Bendixson theorem. We omit the details but offer Fig. 1, which gives the main idea. To be specific, we assume that the inequalities (3.8) hold. We now take limits. Let $I = \bigcap_{m=1}^{\infty} I_m = \bigcap_{m=1}^{\infty} J_m$ and let $\phi(\eta) = \lim_{m\to\infty} \phi_m(\eta)$, $\psi(\eta) = \lim_{m\to\infty} \psi_m(\eta)$ for $\eta \in I$. The estimates (3.7) imply that

$$\phi: I \to [0, \infty), \qquad \psi: I \to (-\infty, 0]$$

are both continuous on I and, also, that for any point $z \in \omega(y_0)$, one has $z^i \in I$, and that either

$$f^i(z^i, z^{i-1}) = \phi(z^i) \qquad \text{or} \qquad f^i(z^i, z^{i-1}) = \psi(z^i)$$

Thus, at most two values of z^{i-1} are possible for such z^i, by the monotonicity of f^i. Now take $z_0 \in \omega(y_0)$ and let $z(t)$ be the solution through this point. The above conclusion and the fact that $t \to (z^i(t), z^{i-1}(t))$ is one-to-one (by Lemma 3.5) imply that $z^i(t)$ can assume any given value $z^i \in \mathbf{R}$ at most twice. Therefore, $z^i(t)$ approaches a limit as $t \to \infty$. As i is arbitrary one sees that $\lim_{t\to\infty} z(t)$ exists and hence is an

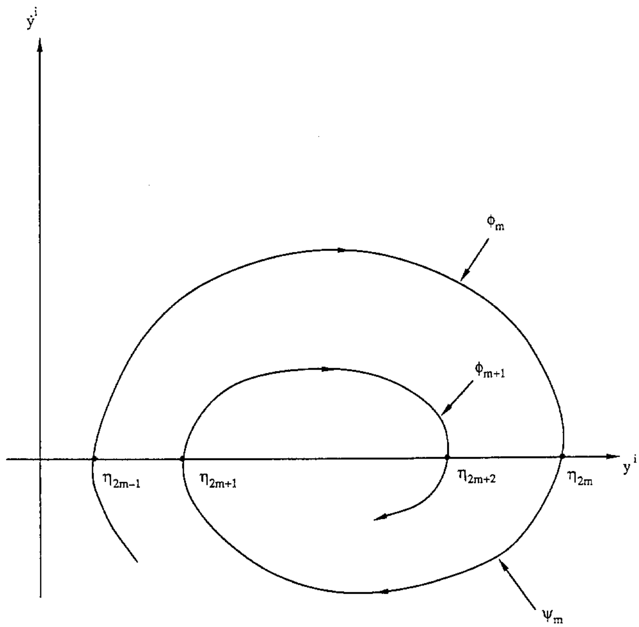

Fig. 1. A nonconstant nonperiodic orbit $y(t)$ in $\omega(x_0)$, as in the proof of Lemma 3.3.

equilibrium point in $\omega(z_0)$. But this contradicts the assumption that $\omega(x_0)$ contains no equilibria. ∎

Corollary 3.7. *Let $B \subset O$ be compact and $\{\gamma_m\} \subset B$ be a sequence of nontrivial periodic orbits such that either*

(a) $\gamma_m < \gamma_{m+1}$, $m \geqslant 1$, *or*

(b) $\gamma_{m+1} < \gamma_m$, $m \geqslant 1$.

Let $\Omega = \{x \in B: x = \lim_{m \to \infty} x_m$ where $x_m \in \gamma_m\}$. Then either Ω is an equilibrium, a nonconstant periodic orbit or a set $E \cup H$ where each $y \in E$ is an equilibrium point and H is a set of orbits homoclinic to/heteroclinic between points of E. Furthermore, for each i the planar projection $\Pi^i: \Omega \to \mathbf{R}^2$ is one-to-one on Ω.

Proof. The set Ω is nonempty. Let $y \in \Omega$ and $y(t)$ be the solution of (3.1) satisfying $y(0) = y$. Let $p_m(t)$ be the solution of (3.1) satisfying $x_m = p_m(0) \in \gamma_m$ where $x_m \to y$. It follows that $p_m(t) \to y(t)$ uniformly on compact intervals. In particular, Ω is an invariant set for (3.1). If Ω consists of a single point, then Ω reduces to an equilibrium. By Theorem 3.2 either Ω consists of a periodic orbit γ and $\gamma_m \to \gamma$, Period $\gamma_m \to$ Period γ or $\liminf_{m \to \infty} \operatorname{dist}(\gamma_m, \gamma) > 0$ for any periodic orbit γ.

Assume that Ω is neither an equilibrium nor a periodic orbit. If y is not an equilibrium point, then for any t, s with $t \neq s$ and

$$y(t) - y(s) \in \mathcal{N}, \qquad N(y(t) - y(s)) = N(p_m(t) - p_m(s)) = k_m$$

for large m. It follows that $k_m = k$, independent of m, for large m, and that $N(y(t) - y(s)) = k$ for all t and s with $t \neq s$. Therefore, $t \to (y^i(t), \dot{y}^i(t))$ is an immersion. Moreover, neither $\alpha(y)$ nor $\omega(y)$ is a periodic orbit, as the γ_m remain bounded away from other periodic orbits. Arguing as in Lemma 3.6 we establish that both $\alpha(y)$ and $\omega(y)$ are equilibria which belong to Ω since the latter is closed. For, in the proof of Lemma 3.6, if $\omega(y)(\alpha(y))$ is not an equilibrium, then $(y^i(t), \dot{y}^i(t))$ must spiral in the plane as in Fig. 1 which would contradict that $\gamma(y)$ consists of points of Ω. Thus we have proved all but the last assertion of Corollary 3.7. If Ω is either an equilibrium or a periodic orbit, then this last assertion is immediate.

Suppose, then, that Ω is the third alternative. If y_1 and y_2 are distinct points of Ω, then there exist sequences $x_{m,1} \to y_1$, $x_{m,2} \to y_2$ with $x_{m,i} \in \gamma_m$. For all large m, $x_{m,1}$ and $x_{m,2}$ are distinct points of γ_m so $N(x_{m,2} - x_{m,1}) = k$ for large m. Let $y_1(t)$ and $y_2(t)$ be the solutions satisfying $y_i(0) = y_i$, $i = 1, 2$. Then $N(y_1(t) - y_2(t)) = k$ for all t for which $y_1(t) - y_2(t) \in \mathcal{N}$. It follows that $N(y_1(t) - y_2(t)) = k$ for all $t \in \mathbf{R}$ and so $N(y_1 - y_2) = k$. Hence $\Pi^i y_1 \neq \Pi^i y_2$ for each i. This proves the last assertion. ∎

Proposition 3.8. *Let $p(t)$ be a nonconstant periodic solution, with orbit $\gamma = \gamma(p_0)$, and suppose the dimension of its center manifold is*

$$\dim W^c \leqslant 2$$

Then any sufficiently small neighborhood U of γ has the following properties. If one has sequences of solutions $x_m(t)$ and numbers $t_m > 0$ satisfying

$$\begin{aligned}
&x_m(0) \in \partial U, \qquad && x_m(t_m) \in \partial U \\
&x_m(t) \in \bar{U} && \text{for } 0 \leqslant t \leqslant t_m \\
&x_m(0) \to x_-, && x_m(t_m) \to x_+ \\
&\min_{0 \leqslant t \leqslant t_m} \operatorname{dist}(x_m(t), \gamma) \to 0 &&
\end{aligned} \tag{3.9}$$

Then

$$x_- \in W^{cs}, \qquad x_+ \in W^{cu} \tag{3.10}$$

both hold. Further, at least of

$$x_- \in W^s \qquad \text{or} \qquad x_+ \in W^u \tag{3.11}$$

holds.

The same result holds if instead $p(t) \equiv p_0$ is an equilibrium point, with a center manifold satisfying the following:

$$\dim W^c \leqslant 2 \tag{3.12}$$

with

$$\begin{aligned}
&\textit{nonzero eigenvalues } \lambda = \pm i\nu \neq 0 \textit{ of } Df(p_0) \\
&\textit{in case } \dim W^c = 2
\end{aligned} \tag{3.13}$$

Proof. For any neighborhood U of γ the assumption (3.9) implies $t_m \to \infty$. From this it follows that the forward orbit through x_- stays entirely in $\bar{U}$, and likewise with the backward orbit through x_+:

$$\gamma^+(x_-), \qquad \gamma^-(x_+) \subset \bar{U}$$

Thus if U is sufficiently small one has $x_- \in W^{cs}$ and $x_+ \in W^{cu}$, and indeed, this conclusion holds irrespective of $\dim W^c$. This in fact proves the theorem if γ is hyperbolic, as $W^{cs} = W^s$ and $W^{cu} = W^u$. Let us therefore assume that γ is not hyperbolic. Let us also assume, for now, that γ is a nonconstant periodic solution and that W^c is orientable; the nonorientable case (a Möbius orbit) is handled similarly. We briefly discuss the case of an equilibrium point at the end of the proof. We therefore have now

$$\dim W^c = 2 \tag{3.14}$$

where one of the two dimensions is given by the tangent to the orbit γ, and the other by a nontrivial characteristic multiplier $\alpha = 1$.

To prove the more difficult part of the Theorem (3.11), we first write the ODE in a special coordinate system in a neighborhood of γ. To begin, consider coordinates $(\xi, \theta) \in \mathbf{R}^{n-1} \times S^1$, where $S^1 = \mathbf{R}/\tau\mathbf{Z}$, where θ represents the angle about γ, and ξ is a coordinate in a transverse hyperplane through γ at $p(\theta)$. Following Hale [17], we take a map

$$(\xi, \theta) \to x = p(\theta) + L(\theta)\,\xi$$

where the linear map $L(\theta)\colon \mathbf{R}^{n-1} \to \mathbf{R}^n$ has range transverse to $\dot{p}(\theta)$. This map takes a neighborhood of $\{0\} \times S^1$ diffeomorphically onto a neighborhood of γ, and so establishes such coordinates. The ODE (3.1) takes the form

$$\begin{aligned} \dot{\xi} &= a(\xi, \theta) \qquad \text{with} \qquad a(0, \theta) \equiv 0 \\ \dot{\theta} &= b(\xi, \theta) \qquad \text{with} \qquad b(0, \theta) \equiv 1 \end{aligned} \tag{3.15}$$

with $\xi = 0$ corresponding to γ.

We may further assume, by a θ-dependent diffeomorphism of ξ which fixes the origin, that the center-stable manifold W^{cs} of γ, the center-unstable manifold W^{cu}, and hence the center manifold $W^c = W^{cs} \cap W^{cu}$ are precisely linear coordinate subspaces of $\mathbf{R}^{n-1}$ of appropriate dimension. That is, we have $\xi = (\xi^1, \xi^2, \xi_3)$ where in a neighborhood of $\xi = 0$ these manifolds are given by

$$\begin{aligned} &W^{cs}\colon \operatorname{span}\{\xi^1, \xi^2\} && (\text{that is, } \xi^3 = 0) \\ &W^{cu}\colon \operatorname{span}\{\xi^2, \xi^3\} && (\text{that is, } \xi^1 = 0) \\ &W^{c}\colon \operatorname{span}\{\xi^2\} && (\text{that is, } \xi^1 = 0 \text{ and } \xi^3 = 0) \end{aligned}$$

The system (3.15) takes the form

$$\begin{aligned} \dot{\xi}^i &= a^i(\xi^1, \xi^2, \xi^3, \theta), \qquad i = 1, 2, 3 \\ \dot{\theta} &= b(\xi^1, \xi^2, \xi^3, \theta) \end{aligned} \tag{3.16}$$

where the invariance of these manifolds forces

$$\begin{aligned} a^1(0, \xi^2, \xi^3, \theta) &\equiv 0 \\ a^3(\xi^1, \xi^2, 0, \theta) &\equiv 0 \end{aligned} \tag{3.17}$$

We recall the invariant foliation of W^{cs}, transverse to W^c. This is given by the family of maps

$$\begin{aligned} \xi^2 &= \phi(\xi^1, \xi^2_*, \theta_*) \qquad \text{with} \qquad \phi(0, \xi^2_*, \theta_*) = \xi^2_* \\ \theta &= \psi(\xi^1, \xi^2_*, \theta_*) \qquad \text{with} \qquad \psi(0, \xi^2_*, \theta_*) = \theta_* \end{aligned}$$

For each fixed (ξ^2_*, θ_*), the graph of (ϕ, ψ) in W^{cs} is a leaf of the foliation, and near γ leaves are mapped into one another by the flow. A new coordinate system $(\bar{\xi}, \bar{\theta})$ given by

$$\bar{\xi}^1 = \xi^1, \; \bar{\xi}^2 = \phi(\xi^1, \xi^2, \theta), \; \bar{\xi}^3 = \xi^3, \; \bar{\theta} = \psi(\xi^1, \xi^2, \theta)$$

transforms the leaves to affine spaces:

$$\bar{\xi}^2 = \text{constant}, \qquad \bar{\theta} = \text{constant}$$

in W^{cs} (that is, in the space $\bar{\xi}^3 = 0$). Invariance of this foliation implies, in the new coordinates, that $\dot{\bar{\xi}}^2$ and $\dot{\bar{\theta}}$ are independent of $\bar{\xi}^1$ when $\bar{\xi}^3 = 0$. That is, the functions a^2 and b satisfy (we now drop the bars)

$$\begin{aligned} a^2(\xi^1, \xi^2, 0, \theta) &= a^2(0, \xi^2, 0, \theta) \\ b(\xi^1, \xi^2, 0, \theta) &= b(0, \xi^2, 0, \theta) \end{aligned} \tag{3.18}$$

A similar transformation of the invariant foliation in W^{cu} yields

$$\begin{aligned} a^2(0, \xi^2, \xi^3, \theta) &= a^2(0, \xi^2, 0, \theta) \\ b(0, \xi^2, \xi^3, \theta) &= b(0, \xi^2, 0, \theta) \end{aligned} \tag{3.19}$$

One must note, in making these normalizing transformations, that previous normalizations are maintained. Thus (3.15), (3.17), (3.18), and (3.19) all hold. The stable and unstable manifolds in these new coordinates are given by

$$\begin{aligned} &W^s: \operatorname{span}\{\xi^1\} \qquad (\text{that is, } \xi^2 = 0 \text{ and } \xi^3 = 0) \\ &W^u: \operatorname{span}\{\xi^3\} \qquad (\text{that is, } \xi^1 = 0 \text{ and } \xi^2 = 0) \end{aligned}$$

At this point it is convenient to use θ, instead of t, as the independent variable; this is justified as $\dot{\theta} = b(\xi, \theta)$ is near unity. The above normalizations continue to hold and, in fact, easily imply that the system (3.16) takes the form

$$\begin{aligned} \frac{d\xi^i}{d\theta} &= u^i(\xi^1, \xi^2, \xi^3, \theta)\, \xi^i, \qquad i = 1, 3 \\ \frac{d\xi^2}{d\theta} &= c(\xi^2, \theta) + r(\xi^1, \xi^2, \xi^3, \theta) \end{aligned} \tag{3.20}$$

Here u^i are square matrices of appropriate size and the function r vanishes if either $\xi^1 = 0$ or $\xi^3 = 0$; thus

$$r(\xi^1, \xi^2, \xi^3, \theta) = 0(|\xi^1|\ \ |\xi^3|)$$

The equation

$$\frac{d\xi^2}{d\theta} = c(\xi^2, \theta) \tag{3.21}$$

represents the vector field on the center manifold W^c. Of course, $c(0, \theta) \equiv 0$ and $\partial c(0, \theta)/\partial \xi^2 \equiv 0$. We note here that the dimension constraint (3.14) on W^c implies that the variable ξ^2 is a scalar:

$$\xi^2 \in \mathbf{R}$$

That is, (ξ^2, θ) are coordinates on the two-dimensional center manifold. We also note that all characteristic multipliers of the linear system

$$\frac{d\xi^i}{d\theta} = u^i(0, 0, 0, \theta)\, \xi^i$$

are inside the unit circle if $i = 1$ and outside the unit circle if $i = 3$. This immediately yields the estimates

$$\begin{aligned} |\xi^1(\theta + \beta)| &\leqslant K_1 e^{-\mu\beta}\, |\xi^1(\theta)| \\ |\xi^3(\theta)| &\leqslant K_1 e^{-\mu\beta}\, |\xi^3(\theta + \beta)| \end{aligned} \tag{3.22}$$

for solutions to the full nonlinear system (3.20) near $\xi = 0$, for any $\beta \geqslant 0$, where $K_1 > 0$ and $\mu > 0$ do not depend on the solution or on θ or β.

We now complete the proof of our result. Suppose it is false, that is, suppose

$$x_- \in W^{cs} - W^s \qquad \text{and} \qquad x_+ \in W^{cu} - W^u \tag{3.23}$$

Let $\xi_m(\theta)$ denote the solution, as a function of θ, as in the statement of the proposition. Here $\theta_m \leqslant \theta \leqslant \theta_m + \beta_m$ for some θ_m and β_m, and where $\xi_m(\theta_m)$ and $\xi_m(\theta_m + \beta_m)$ correspond to $x_m(0)$, $x_m(t_m)$, respectively, and

$$\beta_m \to \infty$$

Assume without loss that θ_m is bounded (as it is determined mod τ) and that $\theta_m \to \theta_\infty$. One has also

$$\xi_m(\theta_m) \to \xi_-, \qquad \xi_m(\theta_m + \beta_m) \to \xi_+$$

and (3.23) implies

$$\xi_-^2 \neq 0 \qquad \text{and} \qquad \xi_+^2 \neq 0 \tag{3.24}$$

Finally, the estimates (3.22) yield

$$\begin{aligned} |\xi_m^1(\theta)| &\leqslant K_1 e^{-\mu(\theta - \theta_m)} |\xi_m^1(\theta_m)| \\ |\xi_m^3(\theta)| &\leqslant K_1 e^{-\mu(\theta_m + \beta_m - \theta)} |\xi_m^3(\theta_m + \beta_m)| \end{aligned}$$

hence

$$|r(\xi_m(\theta), \theta)| \leqslant K_2 e^{-\mu\beta_m}$$

uniformly for $\theta_m \leqslant \theta \leqslant \theta_m + \beta_m$ and some $K_2 > 0$.

Let $\tilde{\xi}_m^2(\theta)$ denote the solution of the center manifold equation (3.21) with the initial condition $\tilde{\xi}^2(\theta_m) = \xi_m^2(\theta_m)$, and suppose $\bar{U}$ is contained in a neighborhood V in which the Lipschitz constant of $c(\xi^2, \theta)$ with respect to ξ^2 is at most $\mu/2$:

$$\left| \frac{\partial c(\xi^2, \theta)}{\partial \xi^2} \right| \leqslant \frac{\mu}{2}$$

This is easily achieved by taking U and V small enough. A straightforward application of Gronwall's inequality now yields

$$|\xi_m^2(\theta) - \tilde{\xi}^2(\theta)| \leqslant \frac{2K_2}{\mu} e^{-\mu\beta_m}(e^{\mu\beta_m/2} - 1)$$

in the range $\theta_m \leqslant \theta \leqslant \theta_m + \beta_m$ for all large m, so

$$\max_{\theta_m \leqslant \theta \leqslant \theta_m + \beta_m} |\xi_m^2(\theta) - \tilde{\xi}_m^2(\theta)| \to 0$$

One also has

$$\min_{\theta_m \leqslant \theta \leqslant \theta_m + \beta_m} |\xi_m^2(\theta)| \to 0$$

by (3.9), and hence

$$\min_{\theta_m \leqslant \theta \leqslant \theta_m + \beta_m} |\tilde{\xi}^2_m(\theta)| \to 0 \tag{3.25}$$

We now arrive at a contradiction. As $\tilde{\xi}^2_m(\theta)$ satisfies the scalar equation (3.21), its minimum norm must occur near one of the end points $\theta = \theta_m$ or $\theta_m + \beta_m$. More precisely, for any m the sequence $\{\tilde{\xi}^2_m(\theta_m + j\tau\}$ for $0 \leqslant j \leqslant [\beta_m/\tau]$ is either strictly increasing in j, strictly decreasing in j, or constant in j; this follows from the periodicity of $c(\xi^2, \theta)$ in θ, and from elementary considerations in the two-dimensional (ξ^2, θ)-phase plane. In view of (3.25), therefore, one has

$$\min\{|\tilde{\xi}^2_m(\theta_m)|, |\tilde{\xi}^2_m(\theta_m + \beta_m)|\} \to 0$$

and so either $\xi^2_- = 0$ or $\xi^2_+ = 0$. But this contradicts (3.24), so completes the proof of the proposition in the case γ is a periodic orbit.

In case γ is an equilibrium, the proof is essentially the same except that the angle θ is absent. One uses the original variable t as the independent variable in the ξ-equations and so obtains

$$\min_{0 \leqslant t \leqslant t_m} |\tilde{\xi}^2_m(t)| \to 0$$

for the solution of the center manifold equation

$$\dot{\xi}^2 = c(\xi^2) \tag{3.26}$$

The assumptions (3.12), (3.13) that ξ^2 either is a scalar or is two-dimensional with a center for the linearization of (3.26) at $\xi^2 = 0$ now come into play. They imply, again by elementary phase portrait arguments, that

$$\min\{|\tilde{\xi}^2_m(0)|, |\tilde{\xi}^2_m(t_m)|\} \to 0$$

as before, this leads to a contradiction. ∎

Lemma 3.9. *Let $p(t)$ be a nonconstant periodic solution, with orbit $\gamma = \gamma(p_0)$ and minimal period $\tau > 0$. Let k_0 denote the constant value $N(\dot{p}(t)) \equiv k_0$. If there is a nontrivial center manifold W^c for γ, then there exists $\varepsilon > 0$ such that for any sufficiently small neighborhood U of γ, one has*

$$x - y \in \mathcal{N} \qquad \text{and} \qquad N(x - y) = k_0$$

whenever, x, $y \in U$ are distinct points satisfying $y \in \gamma$ and

$$\operatorname{dist}(x, W^c) \leqslant \varepsilon \operatorname{dist}(x, \gamma).$$

If p_0 is an equilibrium which possesses a nontrivial center manifold, then there exist an integer k_0 and a quantity $\varepsilon > 0$ such that for any sufficiently small neighborhood U of p_0, one has

$$x - p_0 \in \mathcal{N} \qquad \textit{and} \qquad N(x - p_0) = k_0$$

whenever $x \in U$ satisfies

$$x \neq p_0$$

and

$$\operatorname{dist}(x, W^c) \leqslant \varepsilon \operatorname{dist}(x, p_0).$$

Proof. Suppose the lemma is false, for some (nonhyperbolic) orbit γ. We assume that γ is a nonconstant periodic orbit; the case of an equilibrium γ is similar and, so, is omitted. There exist then sequences

$$x_m \to \gamma, \qquad x_m \neq y_m \in \gamma,$$
$$\operatorname{dist}(x_m, W^c) \leqslant \varepsilon_m \operatorname{dist}(x_m, \gamma) \qquad \text{for some } \varepsilon_m \to 0. \tag{3.27}$$

such that for each m, either

$$x_m - y_m \notin \mathcal{N}$$

or

$$x_m - y_m \in \mathcal{N} \qquad \text{but} \qquad N(x_m - y_m) \neq k_0.$$

Without loss

$$x_m \to x_0 \in \gamma \qquad \text{and} \qquad y_m \to y_0 \in \gamma;$$

also, we assume that $x_0 = p(0)$, for simplicity. Proposition 3.1 and the openness of $\mathcal{N}$ imply that $x_0 = y_0$, otherwise $N(x_m - y_m) = k_0$ would hold for large m. With this and (3.27), we have

$$z_m \to z_0 \in T_{x_0} W^c, \qquad z_0 \neq 0$$

where

$$z_m = \frac{x_m - y_m}{|x_m - y_m|};$$

here $T_{x_0} W^c$ denotes the tangent space of the center manifold at x_0. Therefore $z_0 \in \mathcal{G}_1 - \{0\}$, with the subspace $\mathcal{G}_1$ corresponding to the variational equation $\dot{z} = Df(p(t))\, z$, and characteristic multipliers of modulus $\sigma = 1$. But also one has $\dot{p}(0) \in \mathcal{G}_1 - \{0\}$, so

$$z_0 \in \mathcal{N} \qquad \text{and} \qquad N(z_0) = N(\dot{p}(0)) = k_0$$

by Lemma 2.2. Thus for large m

$$z_m \in \mathcal{N} \qquad \text{hence} \qquad x_m - y_m \in \mathcal{N}$$

and

$$N(x_m - y_m) = N(z_m) = N(z_0) = k_0,$$

a contradiction. ▮

Lemma 3.10. *Let $p_0 \in \omega(x_0)$ and suppose the solution $p(t)$ through p_0 is either a nonconstant periodic solution or else an equilibrium point. Assume, moreover, that*

$$\Delta \det(-W) < 0 \tag{3.28}$$

if p_0 is an equilibrium, where $W = D(f(p_0))$. Then in fact

$$\omega(x_0) = \gamma(p_0)$$

Proof. Suppose $\omega(x_0)$ properly contains $\gamma(p_0)$; then there is a neighborhood U of $\gamma(p_0)$ such that the solution $x(t)$ through x_0 repeatedly enters and leaves U. One has quantities $s_m \to \infty$ and $t_m > 0$ such that

$$x(s_m) \in \partial U, \qquad x(s_m + t_m) \in \partial U,$$

$$x(t) \in \bar{U} \qquad \text{for} \qquad s_m \leqslant t \leqslant s_m + t_m$$

$$\min_{s_m \leqslant t \leqslant s_m + t_m} \operatorname{dist}(x(t), \gamma(p_0)) \to 0,$$

$$s_m + t_m < s_{m+1}$$

and without loss

$$x(s_m) \to x_-, \qquad x(s_m + t_m) \to x_+.$$

We also assume without loss that U is small enough for the conclusions of Proposition 3.8 and Lemma 3.9 to hold. Now the linear theory of Section 2, applied to the variational equation along $p(t)$, shows that $\dim W^c \leqslant 2$ for the center manifold W^c of $\gamma(p_0)$. The solutions $x_m(t)$ given by

$$x_m(t) = x(s_m + t)$$

therefore satisfy the hypotheses of Proposition 3.8 [in particular, (3.28) implies (3.13) in case p_0 is an equilibrium], and so the conclusions (3.10) and (3.11) hold.

To be specific assume

$$x_- \in W^s \qquad \text{and} \qquad x_+ \in W^{cu}.$$

Let us also assume, for the time being at least, that $p(t)$ is a nonconstant periodic solution with least period $\tau > 0$ and $\dim W^c = 2$. The solution through x_-, denoted $y(t)$ here, then stays in $\bar{U}$ for forward time and approaches $\gamma(p_0)$ exponentially fast, with asymptotic phase:

$$y(t) \in \bar{U} \qquad \text{for all } t \geqslant 0,$$
$$|y(t) - p(t + \theta_-)| \leqslant K e^{-\mu t} \qquad \text{for all } t \geqslant 0,$$

for some $\theta_- \in \mathbf{R}$, $K > 0$, and $\mu > 0$. Thus, the sequence $y(j\tau - \theta_-)$ approaches $p(0) = p_0$ exponentially fast and hence from a direction in some eigenspace $\mathscr{G}_{\sigma_-}$ with $0 < \sigma_- < 1$:

$$\operatorname{dist}\left(\frac{y(j\tau - \theta_-) - p(0)}{|y(j\tau - \theta_-) - p(0)|}, \mathscr{G}_{\sigma_-}\right) \to 0 \qquad \text{as } j \to \infty.$$

Letting k_- denote the value of N on $\mathscr{G}_{\sigma_-} - \{0\}$, one has

$$N(y(j\tau - \theta_-) - p(0)) = k_- \qquad \text{for large } j.$$

Fix such an integer $j = j_-$. Then since $x(s_m + j_-\tau - \theta_-) \to y(j_-\tau - \theta_-)$ as $m \to \infty$, one has (with $m + 1$ replacing m)

$$N(x(s_{m+1} + j_-\tau - \theta_-) - p(0)) = k_- \qquad \text{for large } m,$$

and hence

$$N(x(s_m + t_m + j_-\tau - \theta_- + \varepsilon) - p(r_m + \varepsilon)) \geqslant k_- \qquad \text{for large } m \tag{3.29}$$

where $0 < |\varepsilon| < \varepsilon_m$, for sufficiently small $\varepsilon_m > 0$, $r_m = s_m + t_m - s_{m+1} < 0$, $r_m + \varepsilon_m \leqslant 0$. The ε is introduced to take account of the possibility that $x(s_m + t_m + j_-\tau - \theta_-) - p(r_m)$ may not be in the domain of N. At this point we pass to a subsequence for which the limit $r_m \to r_\infty \pmod{\tau}$ exists; henceforth, the index m will belong to this subsequence.

Now consider the solution $z(t)$ through $z(0) = x_+$; this solution remains in $\bar{U}$ for all $t \leqslant 0$. We claim that

$$N(z(-j\tau - \theta_-) - p(r_\infty)) < k_-, \qquad \text{for large } j. \tag{3.30}$$

There are several cases. First, if $z(0) = x_+ \notin W^u$, then

$$\frac{\operatorname{dist}(z(t), W^c)}{\operatorname{dist}(z(t), \gamma)} \to 0 \qquad \text{as } t \to -\infty.$$

By Lemma 3.9, the left-hand side of (3.30) equals k_0 for large j and $k_0 < k_-$ (since $\dim W^c = 2$ and by Theorem 2.6). On the other hand, suppose

$z(0)=x_+ \in W^u$. Then as with the solution $y(t)$, the solution $z(t)$ approaches γ with asymptotic phase:

$$|z(t)-p(t+\theta_+)| \leqslant Ke^{\rho t}, \qquad t \leqslant 0$$

for some $\theta_+ \in \mathbf{R}$, $K>0$ and $\rho>0$. If $r_\infty \neq \theta_+ - \theta_-$ (mod τ), then

$$z(-j\tau-\theta_-) \to p(\theta_+ - \theta_-) \neq p(r_\infty)$$

as $j \to \infty$, so again (3.30) holds by Lemma 3.9. Finally, suppose $r_\infty \equiv \theta_+ - \theta_-$ (mod τ); then

$$z(-j\tau-\theta_-) \to p(r_\infty)$$

as $j \to \infty$. As in the corresponding argument for $y(t)$, the convergence of this sequence is along an eigenspace $\mathscr{G}_{\sigma_+}$, with $\sigma_+ > 1$. The left-hand side of (3.30) therefore equals k_+ for large j for some $k_+ < k_0 < k_-$. This again proves (3.30).

Now fix $j=j_+$ such that (3.30) holds. Since $x(s_m+t_m-j_+\tau-\theta_-) \to z(-j_+\tau-\theta_-)$ as $m \to \infty$, and by (3.29) and (3.30) we have

$$k_- > N(z(-j_+\tau-\theta_-)-p(r_\infty)) = N(x(s_m+t_m-j_+\tau-\theta_-)-p(r_m))$$

for all large m. But

$$\begin{aligned} &N(x(s_m+t_m-j_+\tau-\theta_-)-p(r_m)) \\ &\quad \geqslant N(x(s_m+t_m+j_-\tau-\theta_-+\varepsilon)-p(r_m+\varepsilon)) \\ &\quad \geqslant k_- \end{aligned}$$

for suitable ε as in (3.29), providing a contradiction.

Now we consider the modifications in the above argument when $\dim W^c < 2$, that is, when γ is a hyperbolic periodic orbit. Now we have the complication that if k_- is the value of N on a $\mathscr{G}_{\sigma_-} - \{0\}$, $0<\sigma_-<1$, and k_+ is the value of N on a $\mathscr{G}_{\sigma_+} - \{0\}$, $\sigma_+>1$, then $k_-=k_0$ or $k_+=k_0$ are possible *but not both*, where k_0 is as in Lemma 3.9 (k_0 is the value of N on $\mathscr{G}_1 - \{0\}$). If $k_- \neq k_0$, then $k_- > k_0$ and the argument follows the previous one except, of course, that we need only consider that $z(0)=x_+ \in W^u$. If $k_-=k_0$, then $k_+<k_0$ and we must modify the argument above by starting with the solution $z(t)$ through x_+ rather than beginning with the solution $y(t)$ through x_-. Start by obtaining the equality

$$N(z(-j_+\tau-\theta_+)-p(0))=k_+$$

for a fixed large positive integer j_+. This leads to

$$N(x(s_m + t_m - j_+\tau - \theta_+) - p(0)) = k_+$$

for large m, and hence to

$$N(x(s_{m+1} - j_+\tau - \theta_+ + \varepsilon) - p(r_{m+1} + \varepsilon)) \leqslant k_+$$

where now $r_{m+1} = s_{m+1} - (s_m + t_m) > 0$ and $0 < |\varepsilon| < \varepsilon_m$, where $\varepsilon_m > 0$ is chosen sufficiently small so that $r_{m+1} - \varepsilon_m > 0$ and so that the argument of N is in the domain of N. Assume that $r_{m+1} \to r_\infty$ (mod τ) and consider the solution $y(t)$ through $y(0) = x_-$ which remains in $\bar{U}$ for $t \geqslant 0$. The claim is that

$$N(y(j\tau - \theta_+) - p(r_\infty)) \geqslant k_0 \tag{3.31}$$

for large positive integers j. The claim is established in the same way as (3.30). Now fix $j = j_-$ so that (3.31) holds and obtain

$$N(x(s_{m+1} + j_-\tau - \theta_+) - p(r_{m+1})) \geqslant k_0$$

for large m. We then have the contradiction

$$\begin{aligned} k_+ &\geqslant N(x(s_{m+1} - j_+\tau - \theta_+ + \varepsilon) - p(r_{m+1} + \varepsilon)) \\ &\geqslant N(x(s_{m+1} + j_-\tau - \theta_+) - p(r_{m+1})) \\ &\geqslant k_0 \end{aligned}$$

for some large m and suitable ε. This completes the proof of the case that γ is a nontrivial periodic orbit.

If p_0 is an equilibrium at which (3.28) holds, then the hypotheses (3.12) and (3.13) of Proposition 3.8 hold. Observe that if p_0 is not hyperbolic, then $\dim W^c = 2$ by virtue of (3.28). Hence, if p_0 is not hyperbolic, we have $k_+ < k_0 < k_-$, where k_0 is as in Lemma 3.9 and k_+, k_- are, respectively, values attained by N on eigenspaces $\mathscr{G}_{\sigma_+}, \mathscr{G}_{\sigma_-}$, $0 < \sigma_- < 1 < \sigma_+$. If p_0 is hyperbolic, then since (3.28) implies that $Df(p_0)$ has an even number of eigenvalues with positive real part when $\Delta = -1$, or an odd number of such eigenvalues when $\Delta = +1$, one has $k_- > k_+$ by Theorem 2.6. With the above considerations in mind, the argument proceeds as in the periodic case above with the simplification that $p(t) \equiv p_0$. ∎

Lemma 3.11. *Suppose $\alpha(y_0) \cap \omega(y_0) \neq \phi$ for some $y_0 \in \omega(x_0)$. Then the orbit $\gamma(y_0)$ is either an equilibrium, a periodic orbit, or an orbit homoclinic to an equilibrium z_0, that is,*

$$\alpha(y_0) = \omega(y_0) = \{z_0\}.$$

Proof. Assume that $\gamma(y_0)$ is neither an equilibrium nor a periodic orbit. We may also assume without loss that for the first coordinate $y^1(t)$ either

$$\liminf_{t\to-\infty} y^1(t) < \limsup_{t\to-\infty} y^1(t) \qquad \text{or} \tag{3.32}$$

$$\liminf_{t\to\infty} y^1(t) < \limsup_{t\to\infty} y^1(t). \tag{3.33}$$

This follows by arguing as in the proof of Lemma 3.6: if (3.32) and (3.33) were both false, so the limits $y^1(t)\to y^1_\pm$ existed as $t\to\pm\infty$, then in fact $\lim_{t\to\pm\infty} y(t)=y_\pm$ would both exist. Thus $\alpha(y_0)$ and $\omega(y_0)$ would be singleton sets, so $\gamma(y_0)$ would be homoclinic as $\alpha(y_0)\cap\omega(y_0)\neq\phi$. By Lemma 3.5 the map $t\to(y^1(t),\dot{y}^1(t))$ is an immersion. This, the fact that either (3.32) or (3.33) holds, and elementary arguments in the $(y^1,\dot{y}^1)$-plane (see Fig. 1 again) imply that if $\eta\in\alpha(y_0)$ and $\xi\in\omega(y_0)$, then $(\eta^1,\dot{\eta}^1)\neq(\xi^1,\dot{\xi}^1)$. Here $\dot{\eta}^1$ and $\dot{\xi}^1$ denote the numbers $\dot{\eta}^1=f^1(\eta^1,\eta^n)$ and $\dot{\xi}^1=f^1(\xi^1,\xi^n)$. Thus $(\eta^1,\eta^n)\neq(\xi^1,\xi^n)$ for such points, hence $\alpha(y_0)\cap\omega(y_0)=\phi$, a contradiction. ∎

Corollary 3.12. *If $\gamma(x_0)$ is not an equilibrium or periodic orbit, then $\gamma(x_0)\cap\omega(x_0)=\phi$.*

Proof. If $\gamma(x_0)$ is not an equilibrium or periodic orbit, but $\gamma(x_0)\cap\omega(x_0)\neq\phi$, then $\gamma(x_0)\subset\omega(x_0)$, hence $\alpha(x_0)\cap\omega(x_0)\neq\phi$. Thus $\gamma(x_0)$ is homoclinic to some equilibrium by Lemma 3.11 with $y_0=x_0\in\omega(x_0)$. But then $\gamma(x_0)\cap\omega(x_0)=\phi$, a contradiction. ∎

We assume from now on that $\gamma(x_0)$ is neither a single equilibrium nor a periodic orbit. For any $y_0\in\omega(x_0)$ define the integer

$$k(y_0)=\lim_{t\to\infty} N(x(t)-y(t)).$$

By Corollary 3.12, $x(t)\neq y(t)$, so $k(y_0)$ is well defined.

Lemma 3.13. *If y_0, $z_0\in\omega(x_0)$ are distinct points, and y_0 is an equilibrium, then $z_0-y_0\in\mathscr{N}$ and*

$$N(z_0-y_0)=k(y_0) \tag{3.34}$$

Furthermore, the integer $k(y_0)$ is independent of the equilibrium point $y_0\in\omega(x_0)$.

Proof. Fix $t\in\mathbf{R}$ so that $z(t)-y_0\in\mathscr{N}$, and let $t_m\to\infty$ be such that $x(t_m)\to z_0$. Then as N is locally constant, $x(t+t_m)\to z(t)$, and

$y(t+t_m)=y_0$, the definition of $k(y_0)$ implies $N(z(t)-y_0)=k(y_0)$. Thus $z(t)-y_0\in\mathcal{N}$ for all $t\in\mathbf{R}$ by Proposition 1.1, and setting $t=0$ yields (3.34).

To prove that $k(y_0)$ is independent of the equilibrium point $y_0\in\omega(x_0)$, we have, if $z_0\in\omega(x_0)$ is another equilibrium,

$$\begin{aligned} k(y_0) &= N(z_0-y_0) \\ &= N(y_0-z_0)=k(z_0). \quad \blacksquare \end{aligned}$$

When $\omega(x_0)$ contains at least one equilibrium y_0 [equivalently, when $\omega(x_0)$ is not a periodic orbit, by Lemmas 3.6 and 3.10], we denote by k_∞ the common value

$$k_\infty=k(y_0), \qquad y_0\in\omega(x_0) \qquad \text{is an equilibrium.}$$

From now on we make the additional assumption that $\omega(x_0)$ contains an equilibrium.

Lemma 3.14. *Suppose $k(y_0)\neq k_\infty$ for some $y_0\in\omega(x_0)$. Let $t_m\to\infty$ be such that the limits $x(t_m)\to z_0$ and $y(t_m)\to w_0$ both exist. Then if either z_0 or w_0 is an equilibrium, one has $z_0=w_0$.*

Proof. Suppose that at least one of z_0 or w_0 is an equilibrium, but $z_0\neq w_0$. Then from the definition of $k(y_0)$, and from Corollary 3.12, one has

$$\begin{aligned} k(y_0) &= \lim_{m\to\infty} N(x(t_m)-y(t_m)) \\ &= N(z_0-w_0)=k_\infty. \end{aligned}$$

This is a contradiction. $\blacksquare$

Lemma 3.15. *$k(y_0)=k_\infty$ for all $y_0\in\omega(x_0)$.*

Proof. Suppose $k(y_0)\neq k_\infty$ for some $y_0\in\omega(x_0)$ (so y_0 is not an equilibrium), and let $z_0\in\alpha(y_0)$ be an equilibrium point; such exists by Lemma 3.6. As $\alpha(y_0)\subset\omega(x_0)$, one has $x(t_m)\to z_0$ for some $t_m\to\infty$, and hence $y(t_m)\to z_0$ by Lemma 3.14. Thus $z_0\in\alpha(y_0)\cap\omega(y_0)\neq\phi$, and so the orbit $\gamma(y_0)$ is homoclinic to z_0, by Lemma 3.11. But then $y(t)\to z_0$ as $t\to\infty$, and one concludes from Lemma 3.14 that also $x(t)\to z_0$ as $t\to\infty$. Thus $\omega(x_0)=\{z_0\}$, hence $y_0=z_0$ is an equilibrium, a contradiction. $\blacksquare$

Recall for $T\in\mathbf{R}$ the semiorbit

$$\gamma^{T+}(x_0)=\{x(t)\mid t\geqslant T\}$$

whose closure is

$$\overline{\gamma^{T+}(x_0)} = \gamma^{T+}(x_0) \cup \omega(x_0).$$

Lemma 3.16. *There exists $T \geqslant 0$ such that for any distinct points $y_0, z_0 \in \overline{\gamma^{T+}(x_0)}$, one has*

$$z_0 - y_0 \in \mathcal{N}$$

and

$$N(z_0 - y_0) = k_\infty.$$

Proof. For each $t \geqslant 0$ let

$$O_t = \{y_0 \in \omega(x_0) \mid x(t) - y(t) \in \mathcal{N} \quad \text{and} \quad N(x(t) - y(t)) = k_\infty\}.$$

Then O_t is open in $\omega(x_0)$, and in view of Lemma 3.15 one has $O_{t_2} \supset O_{t_1}$ if $t_1 \leqslant t_2$, and $\bigcup_{t \geqslant 0} O_t = \omega(x_0)$. Thus $O_T = \omega(x_0)$ for some $T \geqslant 0$ by compactness of $\omega(x_0)$, and this establishes the result for $y_0 \in \omega(x_0)$ and $z_0 \in \gamma^{T+}(x_0)$.

If both y_0, $z_0 \in \omega(x_0)$, with $y_0 \neq z_0$, let $t \in \mathbf{R}$ be such that $z(t) - y(t) \in \mathcal{N}$. Then there exists $w_0 \in \gamma^{T+}(x_0)$ sufficiently close to $z(t)$ that $w_0 - y(t) \in \mathcal{N}$ and

$$N(z(t) - y(t)) = N(w_0 - y(t)) = k_\infty.$$

Thus $N(z(t) - y(t))$ does not drop in value, hence both $z(t) - y(t) \in \mathcal{N}$ and $N(z(t) - y(t)) = k_\infty$ hold for all $t \in \mathbf{R}$. Setting $t = 0$ establishes the result for $y_0, z_0 \in \omega(x_0)$.

Now consider the remaining case, with distinct points $y_0, z_0 \in \gamma^{T+}(x_0)$, say $y_0 = x(t)$ and $z_0 = x(t + \theta)$ for some $t \geqslant T$ and $\theta > 0$. First, observe that if θ is sufficiently large, then

$$N(x(t + \theta) - x(t)) = k_\infty \qquad \text{for all } t \geqslant T. \tag{3.35}$$

That this holds at $t = T$ follows from the earlier part of this proof and the fact that $x(T + \theta)$ is near $\omega(x_0)$ for large θ. With such θ fixed, there exist arbitrarily large t such that $x(t)$ and $x(t + \theta)$ are close to distinct non-equilibrium points of $\omega(x_0)$ (with such points not lying on an orbit of period θ), so again from above one has the equality (3.35) for large t. Therefore, for sufficiently large θ, say $\theta \geqslant \theta_0 > 0$, (3.35) holds as stated.

Next, consider $0 < \theta \leqslant \theta_0$; for this range of θ we allow the possibility of increasing T. Given a lower bound $\theta \geqslant \theta_* > 0$, there exist $T \geqslant 0$ such that (3.35) holds whenever $\theta_* \leqslant \theta \leqslant \theta_0$. Indeed, arguing as in the above paragraph proves this.

Suppose now that (3.35) fails for each $T \geqslant 0$. Then there exist $t_m \to \infty$ and, from above, $\theta_m \to 0$, such that for each m

$$N(x(t_m + \theta_m) - x(t_m)) \neq k_\infty. \tag{3.36}$$

Without loss $x(t_m), x(t_m + \theta_m) \to w_0$ for some nonequilibrium point $w_0 \in \omega(x_0)$. Now $N(w(t+\theta) - w(t)) = k_\infty$ for any t and nonzero θ, hence

$$N(\dot{w}(t)) = N(\theta^{-1}[w(t+\theta) - w(t)]) = k_\infty$$

whenever $\dot{w}(t) \in \mathcal{N}$ and θ is small. Thus $\dot{w}(t) \in \mathcal{N}$ and $N(\dot{w}(t)) = k_\infty$ for all $t \in \mathbf{R}$. Therefore, as $\theta_m^{-1}[x(t_m + \theta) - x(t_m)]$ is near $\dot{w}(0)$ for large m, one has

$$N(x(t_m + \theta_m) - x(t_m)) = N(\theta_m^{-1}[x(t_m + \theta_m) - x(t_m)]) = N(\dot{w}(0)) = k_\infty. \tag{3.37}$$

Equation (3.37) now contradicts equation (3.36), completing the proof of the Lemma. ∎

Proof of the Main Theorem. (a) Assume that neither (i) nor (ii) in the statement of the theorem holds, that is, $\omega(x_0)$ neither is a single equilibrium nor is a nonconstant periodic orbit. Then Lemma 3.10 implies that $\omega(x_0)$ does not contain a nonconstant periodic orbit and that for each equilibrium $z_0 \in \omega(x_0)$ one has $\Delta \det(-Df(z_0)) \geqslant 0$.

Now fix a nonequilibrium point $y_0 \in \omega(x_0)$; we must show

$$\omega(y_0) = \{z_0\} \tag{3.38}$$

is a single equilibrium, and likewise with $\alpha(y_0)$. Considering only $\omega(y_0)$ (as the proof for $\alpha(y_0)$ is similar), one sees by arguing as in the proof of Lemma 3.6 that (3.38) holds if $\lim_{t \to \infty} y^i(t)$ exists for some i. Therefore, assume to the contrary that $\lim_{t \to \infty} \inf y^i(t) < \lim_{t \to \infty} \sup y^i(t)$ for each i; this and Lemma 2.2 immediately yield the spiraling trajectory depicted in Fig. 1. Next consider a Jordan curve $\mathcal{J}$ in the $(x^i, \dot{x}^i)$-plane (for some i) as depicted in Fig. 2. Much as in the proof of the classical Poincaré–Bendixson theorem, the curve $\mathcal{J}$ consists of a vertical line segment AB disjoint from the horizontal axis, together with a segment of the trajectory $(y^i(t), \dot{y}^i(t))$ joining A and B. Let

$$C = (y^i(t_1), \dot{y}^i(t_1)) \in \mathcal{J}_{\text{ext}},$$
$$D = (y^i(t_2), \dot{y}^i(t_2)) \in \mathcal{J}_{\text{int}}$$

denote two points on the trajectory [more precisely, the planar projection of the trajectory $\gamma(y_0)$] which are in the exterior and interior, respectively, of $\mathcal{J}$; again, see Fig. 2.

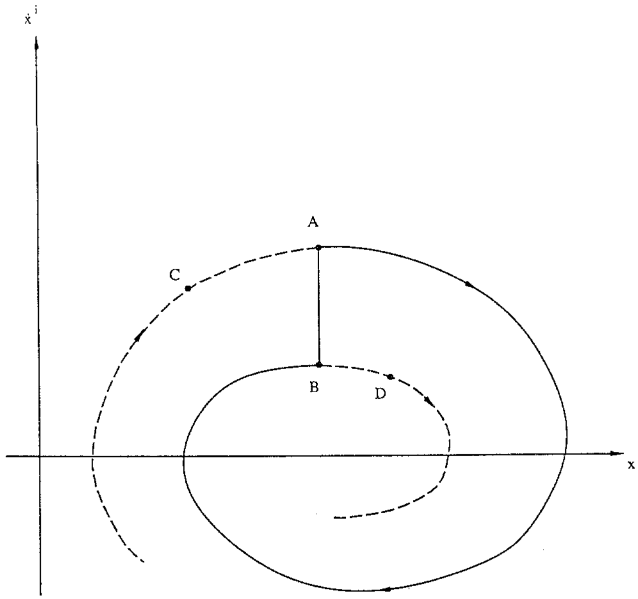

Fig. 2. The Jordan curve $\mathscr{J}$ consists of the vertical segment AB together with a portion of the $(y^i(t), \dot{y}^i(t))$ trajectory (solid) joining A to B. The dashed curve denotes that part of the trajectory which is exterior or interior to $\mathscr{J}$.

By Lemma 3.16, for any $t \geqslant T$ the point $(x^i(t), \dot{x}^i(t))$ cannot lie on the part of $\mathscr{J}$ composed of the trajectory $\gamma(y_0)$. Further, $(x^i(t), \dot{x}^i(t))$ can cross the vertical segment AB in only one direction, left to right in the case of Fig. 2, as AB lies entirely above or entirely below the horizontal axis. Therefore, $(x^i(t), \dot{x}^i(t))$ cannot meet $\mathscr{J}$ for all large t, say

$$(x^i(t), \dot{x}^i(t)) \notin \mathscr{J} \qquad \text{for all } t \geqslant T_*$$

for some T_*, and must eventually lie in one of the two regions $\mathscr{J}_{\text{ext}}$ (the exterior) or $\mathscr{J}_{\text{int}}$ (the interior). But this contradicts the fact that the point $(x^i(t), \dot{x}^i(t))$ must repeatedly return to neighborhoods of both C and D, since $y_0 \in \omega(x_0)$. With this contradiction, the proof that $\omega(x_0)$ is a single equilibrium is complete.

To complete the proof of (a), again assume that (i) and (ii) both fail, and let k_∞ be the integer in the statement of Lemma 3.16. As k_∞ is in the range of N, its parity is as claimed; to be specific assume $\Delta = -1$ so that k_∞ is odd. (We omit the proof of the case $\Delta = +1$ as it is similar.) Fix $z_0 \in E$, that is, $z_0 \in \omega(x_0)$ is an equilibrium, and let

$$k_* = \text{card}\,\{\lambda \mid \lambda \text{ is an eigenvalue of } Df(z_0) \text{ satisfying } \operatorname{Re} \lambda > 0\}$$

counting multiplicity. We must show $k_* = k_\infty - 1$ or k_∞.

First, consider the case that z_0 is a nonisolated point of E, that is, there exist $E\backslash\{z_0\} \supset \{z_m\}_{m=1}^{\infty}$ such that $z_m \to z_0$ as $m \to \infty$. Then, by taking a subsequence if necessary, we may assume that

$$\frac{z_m - z_0}{|z_m - z_0|} \to w_0 \qquad \text{as } m \to \infty$$

where $Df(z_0)\, w_0 = 0$ and $w_0 \neq 0$. It follows from the theory in Section 2 that $w_0 \in \mathcal{N}$ and

$$N(w_0) = \begin{cases} k_*, & k_* \text{ odd} \\ k+1, & k_* \text{ even} \end{cases}$$

On the other hand, from Lemma 3.16 we can conclude that for $m = 1, 2, \ldots$,

$$N(w_0) = N(z_m - z_0) = k_\infty.$$

Thus we have $k_* = k_\infty$ or $k_* = k_\infty - 1$ as asserted. Hereafter, we assume z_0 is an isolated point of E.

As $z_0 \in \omega(x_0) \neq \{z_0\}$, there is a neighborhood $\mathbf{R}^n \supset V$ of z_0 which $x(t)$ repeatedly enters and leaves, staying inside for arbitrarily long times, much as in the statement of Proposition 3.8. In particular one easily obtains a point $z_+ \in \omega(x_0)$ satisfying

$$z_+ \in \partial V,$$
$$\bar{V} \supset \gamma^-(z_+),$$

and hence, provided V is chosen small enough,

$$z_+ \in W^{cu}(z_0).$$

Since z_0 is an isolated point of E, we may assume that V is so small that $\bar{V}$ contains no other point of E. It then follows from an earlier part of the proof that

$$\alpha(z_+) = \{z_0\}. \tag{3.39}$$

By taking an appropriate sequence $t_m \to -\infty$, one has the limit

$$\frac{z_+(t_m) - z_0}{|z_+(t_m) - z_0|} \to w_0$$

where $w_0 \neq 0$ belongs to one of the generalized eigenspaces of $Df(z_0)$ corresponding to an eigenvalue λ with $\operatorname{Re} \lambda \geqslant 0$. It follows that $N(w_0)$ is defined and that, by Lemma 3.16

$$N(w_0) = k_\infty \tag{3.40}$$

If z_0 is hyperbolic, then $-\det(-Df(z_0))>0$ so k_* is odd and $k_\infty = N(w_0) \leqslant k_*$ by the theory in Section 2. Arguing similarly, using Proposition 3.8 to obtain a point $z_- \in \omega(x_0) \cap W^s(z_0)$ different from z_0 and proceeding as above, one obtains $k_\infty \geqslant k_*$. Thus, $k_\infty = k_*$ and we are done. The important point in the case that z_0 is hyperbolic is that N takes the value k_* on eigenspaces of $Df(z_0)$ corresponding to eigenvalues of different signs.

Hereafter, we assume that z_0 is not hyperbolic and argue by contradiction. Thus, assume that

$$k_* \leqslant k_\infty - 2, \tag{3.41}$$

as a contradiction is obtained in a similar manner if one assumes $k_* \geqslant k_\infty + 1$. Let

$$k_\# = \operatorname{card}\{\lambda \mid \lambda \text{ is an eigenvalue of } Df(z_0) \text{ satisfying } \operatorname{Re}\lambda \geqslant 0\}.$$

The theory in Section 2 implies that

$$k_\infty = N(w_0) \leqslant \begin{cases} k_\# - 1, & k_\# \text{ even} \\ k_\#, & k_\# \text{ odd} \end{cases}$$

where w_0 is defined between (3.39) and (3.40). As z_0 is not hyperbolic, $k_\# = k_* + 1$ or $k_\# = k_* + 2$. If $k_\#$ is even, then $k_\infty = N(w_0) \leqslant k_\# - 1 \leqslant k_* + 1 \leqslant k_\infty - 1$, the last inequality by (3.41), and we have a contradiction. If $k_\#$ is odd, then $k_\# = k_* + 1$ for $k_\# = k_* + 2$ implies that both $k_\#$ and k_* are even. Thus,

$$k_\infty = N(w_0) \leqslant k_\# = k_* + 1 \leqslant k_\infty - 1,$$

and again, we have a contradiction. Hence (3.41) cannot hold.

(b) If (i) or (iii) holds, then Lemma 3.16 implies that $z_0 - y_0 \in \mathcal{N}$, hence $\Pi^i z_0 \neq \Pi^i y_0$ by Proposition 1.1, whenever y_0 and z_0 are distinct points in $\overline{\gamma^{T+}(x_0)}$. Similarly, in case (ii) the corresponding result for $\omega(x_0)$ follows from Propositions 3.1 and 1.1.

(c) For nonequilibrium points $y_0 \in \omega(x_0)$ the claim (0.5) follows from either Proposition 3.1 or Lemma 3.5. For points $y_0 \in \gamma^{T+}(x_0)$ (assuming that x_0 is not an equilibrium), one has that $N(\dot{x}(t))$ is constant for all large t, say $t \geqslant T$, hence $\dot{x}(t) \in \mathcal{N}$ for all $t \geqslant T$. Therefore, $\Pi^i \dot{x}(t) \neq (0, 0)$ for all $t \geqslant T$, as claimed.

4. APPLICATIONS

Monotone cyclic feedback systems arise in mathematical models of cellular control systems in which the components x^i represent the concentration of certain molecules in the cell (see Refs. 1, 2, 5–8, 12, 14, 16, 33). The single-loop feedback system

$$\begin{aligned} \dot{y}^1 &= f(y^p) - \alpha^1 y^1 \\ \dot{y}^i &= \beta^i y^{i-1} - \alpha^i y^i, \qquad 2 \leqslant i \leqslant p \end{aligned} \tag{4.1}$$

is considered where

$$\begin{aligned} \alpha^i &> 0, \qquad 1 \leqslant i \leqslant p \\ \beta^i &> 0, \qquad 2 \leqslant i \leqslant p \end{aligned}$$

and $f: \mathbf{R}^+ \to \mathbf{R}^+$ is a smooth function satisfying one of

$$f'(u) > 0 \qquad \text{for } u \geqslant 0 \tag{PF}$$

or

$$f'(u) < 0 \qquad \text{for } u \geqslant 0 \tag{NF}$$

The equations (4.1) represent a cascade of reactions beginning with the transcription of mRNA (y^1) from a single gene and leading to an end-product molecule whose concentration is denoted by y^p. The two cases are distinguished by whether an increase in the end-product concentration has a positive (PF) or negative (NF) effect on the transcription of mRNA, and these cases correspond to $\Delta = +1$ and $\Delta = -1$, respectively, in our theory. Often, delays are introduced to account for transport and transcription delays.

In Refs. 8 and 19, the linear terms in (4.1) have been replaced by Michaelis–Menten-type nonlinearities resulting in the system

$$\begin{aligned} \dot{y}^1 &= f(y^p) - \frac{\alpha^1 y^1}{b^1 + y^1} \\ \dot{y}^i &= \frac{\beta^i y^{i-1}}{d^i + y^{i-1}} - \frac{\alpha^i y^i}{b^i + y^i}, \qquad 2 \leqslant i \leqslant p \end{aligned} \tag{4.2}$$

where d^i, $b^i > 0$ and f satisfies (NF). A typical nonlinearity in (4.1) and (4.2) in case (NF) is assumed is

$$f(u) = \frac{a}{b + u^r}, \qquad r \geqslant 1$$

It is immediate that (4.1) and (4.2) are monotone cyclic feedback systems if either (PF) or (NF) holds. In case (PF) holds, however, (4.1) and (4.2) define cooperative systems in the sense of Hirsch [20–22]. The powerful results available for cooperative systems imply that "almost all" bounded orbits tend to critical points [20, 21]. Hence, we are interested primarily in the case that (NF) holds.

Recently, so-called multigene models with negative feedback have been considered by Banks and Mahaffy [6] and one of us [36], which takes the form (for a three-gene model)

$$
\begin{aligned}
\dot{y}^1 &= f^1(w^m) - \alpha^1 y^1 \\
\dot{y}^i &= \beta^i y^{i-1} - \alpha^i y^i, && 2 \leqslant i \leqslant p \\
\dot{z}^1 &= f^2(y^p) - \gamma^1 z^1 \\
\dot{z}^j &= \eta^j z^{j-1} - \gamma^j z^j, && 2 \leqslant j \leqslant l \\
\dot{w}^1 &= f^3(z^l) - \delta^1 w^1 \\
\dot{w}^k &= \xi^k w^{k-1} - \delta^k w^k, && 2 \leqslant k \leqslant m
\end{aligned}
\tag{4.3}
$$

where α^i, β^i, γ^j, η^j, ξ^k, $\delta^k > 0$ and f^1, f^2, f^3 satisfy (NF). For simplicity, we have displayed the "three-gene" case in (4.3) corresponding to the three (vector) variables y, z, and w. The reader may easily imagine the general case consisting of a positive integer number, G, of genes, where the end product of the qth gene inhibits the transcription of the mRNA associated with the $(q+1)$st gene, $1 \leqslant q$ (mod G). Delays are sometimes introduced in the first terms on the right side of (4.3). One could also replace the linear terms in (4.3) by Michaelis–Menten nonlinearities as in (4.2).

We are interested primarily in (4.1), (4.2), and (4.3) in the absence of delays. The existence of periodic solutions has been the focus of much of the literature on these equations [8, 15, 18, 19, 24, 26, 27, 35, 36, 42, 43]. Such solutions have been suggested as models for circadian rhythms and as a developmental clock during morphogenesis.

Monotone cyclic feedback systems arise in many other fields. an der Heiden [3] considers a neuron model due to Stein *et al.* [41] which is a three-dimensional monotone cyclic feedback system. The article by Hastings *et al.* [19] contains references to several other monotone cyclic feedback systems in the biological literature.

Motivated by cyclic feedback systems in the biological literature, Hastings *et al.* Webster [19] give sufficient conditions for the monotone cyclic feedback system

$$\dot{x}^i = f^i(x^i, x^{i-1}) \; 1 \leqslant i \leqslant n, \qquad i \,(\mathrm{mod}\; n) \tag{4.4}$$

to possess a nonconstant periodic solution in $\mathbf{R}^n_+ = [0, \infty)^n$. They assume that $f \in C^n$ satisfies

$$\frac{\partial f^i}{\partial x^i} < 0 \qquad \text{and} \qquad \frac{\partial f^i}{\partial x^{i-1}} > 0, \qquad 2 \leqslant i \leqslant n$$

and

$$\frac{\partial f^1}{\partial x^n} < 0.$$

In addition, it is assumed that (4.4) possesses a unique steady-state x_* with positive components and that the Jacobian matrix, $Df(x_*)$, possesses at least one eigenvalue with positive real part and $Df(x_*)$ must not have repeated eigenvalues. Additional assumptions are made to ensure that $\mathbf{R}^n_+$ is positively invariant and that solutions are bounded. They conclude the existence of a nonconstant periodic solution in $\mathbf{R}^n_+$.

The following result gives significantly more information than the existence result of Hastings *et al.* and should prove easier to use. We do not require that $f \in C^n$ or that $Df(x_*)$ has no repeated eigenvalues.

Theorem 4.1. *(a) Let (4.4) be a monotone cyclic feedback system in $\mathbf{R}^n_+ = [0, \infty)^n$. Assume that $\mathbf{R}^n_+$ is positively invariant for (4.4) and that it contains a unique critical point x_*. If $\mathbf{R}^n_+ \supset \gamma^+(x_0)$ is bounded, then either (i) $\omega(x_0) = x_*$, (ii) $\omega(x_0)$ is a nonconstant periodic orbit, or (iii) $\omega(x_0)$ consists of x_* together with a collection of orbits homoclinic to x_*. If*

$$\Delta \det(-Df(x_*)) < 0 \tag{4.5}$$

then alternative (iii) cannot occur.

(b) Now assume $\Delta = -1$. Then sufficient conditions for (ii) to occur for a bounded orbit $\gamma^+(x_0)$ [whether or not (4.5) holds] are that $Df(x_*)$ has at least two eigenvalues with positive real part and $x_0 \in U_{k_0}$, where U_{k_0} is described as follows. Let k be the number of eigenvalues of $Df(x_*)$ with strictly positive real part, and set $k_0 = k-1$ for k even, and $k_0 = k-2$ for k odd. Let U_{k_0} consist of all points $x \in \mathbf{R}^n_+$ for which either

(i) $x - x_* \in \mathcal{N}$ and $N(x - x_*) \leqslant k_0$, or

(ii) $x - x_* \notin \mathcal{N}$ but there exists a neighborhood V of x in $\mathbf{R}^n_+$ such that $N(y - x_*) \leqslant k_0$ for all $y \in V \cap \mathcal{N}$.

Then U_{k_0} is a relatively open, positively invariant subset of $\mathbf{R}^n_+$ and is non-empty if either $x_* \in \dot{\mathbf{R}}^n_+$ (the interior of $\mathbf{R}^n_+$), or if $\delta^i = +1$ for all but a single $i = i_0$, say

$$\delta^i = +1, \qquad i \neq i_0,$$

$$\delta^{i_0} = -1.$$

Proof. (a) Once one extends the vector field f, as a monotone cyclic feedback system, to a neighborhood W of the closed set $\mathbf{R}^n_+$, the result follows directly from the Main Theorem in Section 0.

(b) Now consider the set U_{k_0}, with $\Delta = -1$. By Proposition 1.1, it is open and positively invariant. To see that $U_{k_0} \neq \phi$ if $\delta^i = +1$ for all but one index i, one notes that

$$\phi \neq [x_* + \dot{\mathbf{R}}^n_+) \cup (x_* - \dot{\mathbf{R}}^n_+] \cap \mathbf{R}^n_+ \subset U_{k_0}$$

Indeed, if $x - x_* \in \dot{\mathbf{R}}^n_+$, then $x - x_* \in \mathcal{N}$ and $N(x - x_*) = 1 \leqslant k_0$. To see that $U_{k_0} \neq \phi$ if $x_* \in \dot{\mathbf{R}}^n_+$, one replaces $\dot{\mathbf{R}}^n_+$ with an appropriately chosen orthant, K, $\mathbf{R}^n \supset K$ in the above inclusion.

Let $x_0 \in U_{k_0}$, $\gamma^+(x_0)$ be bounded, and $x(t)$ be the solution of (4.4) with $x(0) = x_0$. Suppose $x_* \in \omega(x_0)$. Then by arguing as in Lemma 3.10, we obtain that for arbitrarily large values of t, $N(x(t) - x_*)$ must attain a value attained by N on the real part of the generalized eigenspaces contained in the center-stable subspace of the linear variational equation about x_*. But these values of N exceed k_0, by our choice of k_0 (see Theorem 2.6). Hence, we have a contradiction to Proposition 1.1 since $N(x(t) - x_*) \leqslant k_0$ for all $t \geqslant 0$. This contradiction implies $x_* \notin \omega(x_0)$ and so (ii) must obtain. ∎

Remark 4.1. The inequality (4.5) is equivalent to the inequality

$$\Delta \left[\prod_{i=1}^{n} \left(-\frac{\partial f^i}{\partial x^i} \right) - \prod_{i=1}^{n} \frac{\partial f^i}{\partial x^{i-1}} \right]_{x = x^*} < 0 \tag{4.6}$$

It clearly holds if $\Delta = -1$ and $\partial f^i / \partial x^i \leqslant 0$, $1 \leqslant i \leqslant n$, as happens to be the case in all the examples in this section. Note that we do not assume that (4.5) holds in giving sufficient conditions for (ii) to hold in Theorem 4.1. However, (4.5) implies that the number of eigenvalues with positive real part is even if $\Delta = -1$ and odd if $\Delta = +1$.

Remark 4.2. $\mathbf{R}^n_+$ could be replaced by any other positively invariant closed *convex* domain D containing a single critical point.

Remark 4.3. Let U_1 be defined as in Theorem 4.1, but replacing k_0 with 1. Suppose that the hypotheses of Theorem 4.1(b) hold, $Df(x_*)$ has at least two eigenvalues with positive real part, and $x_0 \in U_1$ is such that $\gamma^+(x_0)$ is bounded. Since U_1 is positively invariant, $\gamma^+(x_0) \subset U_1$ and $\omega(x_0) = \gamma = \{p(t)\colon t \in \mathbf{R}\}$ where $p(t)$ is a nonconstant periodic solution. By Proposition 1.1, $N(\gamma - x_*) \equiv N(p(t) - x_*)$ is independent of t (since $p(t)$ is periodic). It follows from the invariance of U_1 and the fact that $x(t) \to \gamma$ as $t \to \infty$ that

$$N(\gamma - x_*) = 1.$$

More generally, if $x_0 \in U_{k_0}$ and $x(t) \to \gamma$, a closed orbit, then

$$N(\gamma - x_*) \leqslant k_0$$

Remark 4.4. If $\Delta = +1$, then Theorem 4.1(b) holds with appropriate modifications: one needs that $k \geqslant 1$ rather than $k \geqslant 2$, and one sets $k_0 = k - 1$ for k odd, and $k_0 = k - 2$ for k even. Further, $U_{k_0} \neq \phi$ if $\delta^i = +1$ for each i. Such a result, however, is of limited use, as the hypothesis that $\gamma^+(x_0)$ be bounded usually fails. Indeed, by arguing as in Theorem 4.2 below and using the fact that there are no stable periodic orbits (Remark 2.1), one concludes that $\gamma^+(x_0)$ is unbounded for x_0 in a residual (i.e., large) subset of U_{k_0}.

Remark 4.5. In Theorem 4.1(b) the set U_{k_0} can be replaced with the set W_{k_0} consisting of all points $x \in \mathbf{R}^n_+$ for which either (i) $f(x) \in \mathcal{N}$ and $N(f(x)) \leqslant k_0$ or (ii) $f(x) \notin \mathcal{N}$ but there exists a neighborhood V of x in $\mathbf{R}^n_+$ such that $N(f(y)) \leqslant k_0$ for all $y \in V \cap \mathcal{N}$. Here k_0 is the same. (That the same criterion for $W_{k_0} \neq \phi$ holds, however, is not so clear.) One simply replaces $N(x(t) - x^*)$ with $N(\dot{x}(t)) = N(f(x(t)))$ in the proof and makes the crucial observation that on any of the eigenspaces $\mathcal{G}_\sigma$ of the linearized equation at x_*, one has for $0 \neq y \in \mathcal{G}_\sigma$ with $|y|$ small, that

$$N(y) = N(Df(x_*)\, y) = N(f(x_* + y)).$$

Indeed, the first equality holds because $\mathcal{G}_\sigma$ is invariant for the linear map $Df(x_*)$, and the second follows from the linear approximation.

Our next result, which asserts the existence of an orbitally stable periodic orbit, requires some background and definitions. Let $\gamma \subset O$ be a nonconstant, nonhyperbolic periodic orbit of the monotone cyclic feedback system (4.4), and assume that $\Delta = -1$. Define

$$\text{type}\,(\gamma) = (m, \sigma_{\text{int}}, \sigma_{\text{ext}}),$$

the stability type of γ, as follows. First, m is that integer for which

$$\alpha_m = \alpha_{m+1} = 1$$

where $\{\alpha_k\}_{k=1}^n$ are the characteristic multipliers ordered (as usual) so that $|\alpha_k| \geqslant |\alpha_{k+1}|$. When $\Delta = -1$, m is odd. The symbols σ_{int} and σ_{ext} describe whether the flow on the two-dimensional center manifold of γ spirals toward or away from γ, in the interior and exterior of the Jordan curve $\Pi^i\gamma$. To define σ_{int} and σ_{ext}, consider the local center manifold $W^c \cong (-1, 1) \times S^1$ and the projection

$$\Pi^i \colon W^c \cong (-1, 1) \times S^1 \to \mathbf{R}^2,$$

which is a diffeomorphism onto its range (it is one-to-one by Lemma 2.4 and the fact that W^c is tangent to $\mathscr{G}_1$). Let us assume, by a choice of coordinates, that

$$\gamma \cong \{0\} \times S^1,$$

$$\Pi^i((-1, 0) \times S^1) \subset (\Pi^i\gamma)_{\text{int}},$$

$$\Pi^i((0, 1) \times S^1) \subset (\Pi^i\gamma)_{\text{ext}},$$

where $(\Pi^i\gamma)_{\text{int}}$, $(\Pi^i\gamma)_{\text{ext}} \subset \mathbf{R}^2 - \Pi^i\gamma$ are (respectively) the interior and exterior components of the complement of the Jordan curve $\Pi^i\gamma$. We define σ_{int} and σ_{ext} to be the symbols

$$\sigma_{\text{int}}, \sigma_{\text{ext}} \in \{0, +, -\}$$

as follows. If there exists a sequence

$$\gamma_k \subset (-1, 0) \times S^1, \qquad \operatorname{dist}(\gamma_k, \gamma) \to 0$$

of periodic orbits (i.e., there are orbits on W^c which cluster on γ from the "interior"), we set $\sigma_{\text{int}} = 0$. If there exists such a sequence $\gamma_k \subset (0, 1) \times S^1$ whose projections $\Pi^i\gamma_k$ are exterior to $\Pi^i\gamma$, we set $\sigma_{\text{ext}} = 0$.

If, on the other hand, γ is *asymptotically* orbitally stable from the interior, for the flow restricted to W^c [i.e., $\omega(x_0) = \gamma$ for each $x_0 \in (-1, 0) \times S^1$ near $\gamma = \{0\} \times S^1$], we set $\sigma_{\text{int}} = -$. Correspondingly, $\sigma_{\text{ext}} = -$ for exterior stability. Finally, we set $\sigma_{\text{int}} = +$ if $\alpha(x_0) = \gamma$ for each $x_0 \in (-1, 0) \times S^1$ near γ and $\sigma_{\text{ext}} = +$ if $\alpha(x_0) = \gamma$ for each $x_0 \in (0, 1) \times S^1$ near γ.

We observe here that, with $\Delta = -1$, a nonhyperbolic periodic orbit γ is orbitally stable if and only if type $(\gamma) = (m, \sigma_{\text{int}}, \sigma_{\text{ext}})$ where

$$m = 1, \qquad \sigma_{\text{int}} \neq +, \qquad \sigma_{\text{ext}} \neq +.$$

We also observe that for any nonhyperbolic periodic orbit, the attracting set

$$\{x_0 \in O \colon \omega(x_0) = \gamma\}$$

of γ either has nonempty interior or is a set of the first Baire category (a meager set); and that it has nonempty interior if and only if

$$m = 1 \qquad \text{and} \qquad \sigma_{\text{int}} = - \qquad \text{or} \qquad \sigma_{\text{ext}} = -.$$

Theorem 4.2. *Let (4.4) be a monotone cyclic feedback system in $\mathbf{R}^n_+ = [0, \infty)^n$. Assume that $\mathbf{R}^n_+$ is positively invariant for (4.4) and that it contains a unique critical point x_*. Assume also that $\Delta = -1$, that $Df(x_*)$ has at least two eigenvalues with positive real part, and that $U_{k_0} \neq \phi$. Finally, assume that there is a nonempty open subset $\tilde{U} \subseteq U_{k_0}$ such that $\gamma^+(x_0)$ is bounded for each $x_0 \in \tilde{U}$.*

(a) If all periodic orbits of (4.4) are hyperbolic, then there exists an asymptotically stable-periodic orbit.

(b) If there exists a compact set $B \subseteq \tilde{U}$ such that all nonhyperbolic periodic orbits with

$$\text{type}\,(\gamma) = (1, -, +) \text{ or } (1, +, -) \tag{4.7}$$

satisfy $\gamma \subseteq B$, then (4.4) possesses a periodic orbit which is orbitally stable.

Proof. Without loss, the open set $\tilde{U}$ may be assumed to be positively invariant; if not it may be replaced by its forward orbit $\bigcup_{x_0 \in \tilde{U}} \gamma^+(x_0)$. Let us also fix a monotone sequence $K_m \subseteq K_{m+1} \subseteq \tilde{U}$ of compact subsets of $\tilde{U}$, such that $\bigcup_{m=1}^{\infty} K_m = \tilde{U}$.

(a) Assume that all periodic orbits of (4.4) are hyperbolic but that (4.4) does not possess an asymptotically stable orbit. Then for each m, (4.4) has only finitely many periodic orbits satisfying

$$\gamma \subseteq K_m \qquad \text{and} \qquad \text{period}\,(\gamma) \leqslant m$$

and hence possesses only countably many orbits in all. The set of attraction

$$\{x_0 \in \tilde{U} \mid \omega(x_0) = \gamma\}$$

of each such orbit in $\tilde{U}$ is a set of first Baire category; as $\omega(x_0) = \gamma$ for some γ, for each $x_0 \in \tilde{U}$, the Baire category theorem yields a contradiction.

(b) Assume the condition $\gamma \subset B$ for each nonhyperbolic periodic orbit satisfying (4.7) but that (4.4) does not possess an orbitally stable periodic orbit. As in the proof of (a) above, the set of $x_0 \in \tilde{U}$ for which $\omega(x_0)$ is a hyperbolic periodic orbit is a set of first category. Now let $\Gamma \subseteq \tilde{U}$ denote the union of the set of nonhyperbolic periodic orbits for which $|\alpha| > 1$ for at least one (in fact two) characteristic multipliers, and let

$$\Gamma_m = \cup \{\gamma : \gamma \subset K_m \cap \Gamma \text{ and Period } (\gamma) \leqslant m\}$$

Thus, Γ_m is a compact set. Each $\gamma \subset \Gamma_m$ possesses a local center-stable manifold $W^{cs} = W^{cs}(\gamma)$ which has codimension at least two in $\mathbf{R}^n$. As each $\tilde{\gamma} \subset \Gamma_m$ near γ lies in $W^{cs}(\gamma)$, each $W^{cs}(\gamma) \cap \Gamma_m$ is open in the relative topology of Γ_m. Thus Γ_m is contained in a union of finitely many $W^{cs}(\gamma)$, say

$$\Gamma_m \subset \bigcup_{i=1}^{k_m} W^{cs}(\gamma_{m,i}).$$

If $x_0 \in \tilde{U}$ is such that $\omega(x_0) = \gamma \subset \Gamma_m$, then necessarily $x(t) \in W^{cs}(\gamma_{m,i})$ for all large t, for some i. Thus $x_0 \in \gamma^-(W^{cs}(\gamma_{m,i}))$, where $\gamma^-(S) = \bigcup_{y \in S} \gamma^-(y)$ denotes the backward extension of a set S under the flow. As $W^{cs}(\gamma_{m,i})$ and hence $\gamma^-(W^{cs}(\gamma_{m,i}))$ are of first Baire category, it follows that the set of $x_0 \in \tilde{U}$ for which $\omega(x_0) \subset \Gamma$ is a set of first category.

Thus for a residual (i.e., second category) set of $x_0 \in \tilde{U}$, $\omega(x_0)$ is a nonhyperbolic periodic orbit with $|\alpha| \leqslant 1$ for all characteristic multipliers, that is,

$$\text{type } (w(x_0)) = (1, \sigma_{\text{int}}, \sigma_{\text{ext}}).$$

Furthermore,

$$\sigma_{\text{int}} = + \qquad \text{or} \qquad \sigma_{\text{ext}} = +$$

since by assumption there are no orbitally stable periodic orbits. Let $\Psi \subset \tilde{U}$ denote the set of all such orbits and

$$\Psi_m = \cup \{\gamma \colon \gamma \subset K_m \cap \Psi \text{ with Period } (\gamma) \leqslant m\}$$

We claim that Ψ_m contains at most countably many orbits; from this and from the observations following the definition of type (γ), it follows immediately that

$$\text{type } (\omega(x_0)) = (1, +, -) \text{ or } (1, -, +) \tag{4.8}$$

for a residual set of $x_0 \in \tilde{U}$. To prove the countability claim, we associate a distinct rational point $p \in \mathbf{Q} \times \mathbf{Q}$ ($\mathbf{Q}$ the set of rational numbers) to each $\gamma \subset \Psi_m$. Indeed, if, say, $\sigma_{\text{int}} = -$ for such γ, then by Corollary 3.4 for some $\varepsilon > 0$, the neighborhood $\Pi^i((-\varepsilon, 0) \times S^1) \subset (\Pi^i \gamma)_{\text{int}}$ does not contain the image of any other $\tilde{\gamma} \subset \Psi_m$. Any choice of $p \in \Pi^i((-\varepsilon, 0) \times S^1) \cap \mathbf{Q} \times \mathbf{Q}$ for each $\gamma \subset \Psi_m$ with $\sigma_{\text{int}} = -$ yields a set of rational points in one-to-one correspondence with the periodic orbits in Ψ_m with $\sigma_{\text{int}} = -$. A similar conclusion holds with $\sigma_{\text{ext}} = -$.

Thus (4.8) holds for a residual set of $x_0 \in \tilde{U}$; in particular, there must exist at least one nonhyperbolic orbit $\gamma \subset B \subset \tilde{U}$ of type either $(1, +, -)$ or $(1, -, +)$. Note also that all periodic orbits are totally ordered by inclusion (in the sense of the Jordan curve theorem) as $\Pi^i x_* \in (\Pi^i \gamma)_{\text{int}}$ for each

γ (Proposition 3.2). We may write $\gamma < \tilde{\gamma}$, for distinct periodic orbits γ and $\tilde{\gamma}$, to mean that $\Pi^i \gamma \subset (\Pi^i \tilde{\gamma})_{\text{int}}$. Let $\Psi_{\text{in}} \subset B$ and $\Psi_{\text{out}} \subset B$ denote the union of those nonhyperbolic periodic orbits $\gamma \subset B$ satisfying, respectively, type $(\gamma) = (1, +, -)$ and type $(\gamma) = (1, -, +)$; these are saddle-node orbits for which nearby trajectories on the center manifold spiral inward, respectively, outward. Let γ_k be a sequence of periodic orbits satisfying either

$$\gamma_{k+1} \leqslant \gamma_k \in \Psi_{\text{in}} \qquad \text{for each } k, \text{ and}$$

$$\text{for each } \gamma \in \Psi_{\text{in}} \text{ one has } \gamma_k \leqslant \gamma \text{ for all large } k;$$

or

$$\gamma_{k+1} \geqslant \gamma_k \in \Psi_{\text{out}} \text{ for each } k, \text{ and}$$

$$\text{for each } \gamma \in \Psi_{\text{out}} \text{ one has } \gamma_k \geqslant \gamma \text{ for all large } k.$$

Note first that $\text{dist}(\gamma_k, x_*)$ does not tend to zero; for otherwise $\gamma_k \subset W^c(x_*)$ for large k and γ_k would have at least two characteristic multipliers α satisfying $|\alpha| > 1$, corresponding to the unstable eigenvalues of $Df(x_*)$. We claim in fact that dist $(\gamma_k, \gamma_\infty) \to 0$ for some nonconstant periodic orbit $\gamma_\infty \subset B$. If this were false then, by Corollary 3.7, the only alternative remaining is that Ω, the set of limit points of $\{\gamma_k\}$ (see Corollary 3.7), consists of x_* together with a nonempty set of orbits homoclinic to x_*. But $\Omega \subset B$ and $B \subset U_{k_0}$ does not contain x_* so this alternative is not possible. We have established our claim that dist $(\gamma_k, \gamma_\infty) \to 0$ for some nonconstant periodic orbit γ_∞.

To complete the proof of Theorem 4.2, consider type $(\gamma_\infty) = (m, \sigma_{\text{int}}, \sigma_{\text{ext}})$, for this limiting orbit. To be specific assume $\gamma_{k+1} \leqslant \gamma_k$, i.e., that the orbits limit to γ_∞ from the outside. Then either $\sigma_{\text{ext}} = 0$ or (in the case $\gamma_k = \gamma_\infty$ for large k) $\sigma_{\text{ext}} = -$. Certainly $m = 1$ also holds. Necessarily $\sigma_{\text{int}} = +1$, so that γ_∞ is unstable from the inside (otherwise γ_∞ is orbitally stable). Let $z(t)$ be a solution starting from $z(0) = z_0$ where $z_0 \in W^c(\gamma_\infty)$ where $\alpha(z_0) = \gamma_\infty$, hence $\Pi^i z_0 \in (\Pi^i \gamma_\infty)_{\text{int}}$. Then by Lemma 3.9, $N(z(t) - z(s)) = 1$ whenever $t \neq s$ are sufficiently negative, and hence for all $t \neq s$ by monotonicity. Indeed, by letting $t, s \to \pm\infty$ one obtains $N(z_1 - z_2) = 1$ whenever $z_1 \neq z_2$ with $z_1, z_2 \in \overline{\gamma(z_0)} = \gamma(z_0) \cup \alpha(z_0) \cup \omega(z_0)$, where of course $\alpha(z_0) = \gamma_\infty$. As $z_0 \in B \subset \tilde{U} \subset U_{k_0}$, Theorem 4.1(b) implies that $\omega(z_0) = \gamma_*$, a nonconstant periodic orbit in B. Moreover, $\gamma_* < \gamma_\infty$. Since $\gamma(z_0)$ approaches γ_* along $W^{cs}(\gamma_*)$ and in view of the fact that $N(z_1 - z_2) = 1$ for $z_1 \in \gamma_*$ and $z_2 \in \overline{\gamma(z_0)}$, it follows that $|\alpha| \leqslant 1$ for all characteristic multipliers α of γ_*. Thus γ_* is nonhyperbolic (or else it is orbitally stable), $z(t) \in W^c(\gamma_*)$ for large t, and type $(\gamma_*) = (1, \sigma_{\text{int}}, -)$. Therefore $\sigma_{\text{int}} = +$ must hold, contradicting the fact that γ_k is a minimizing sequence of periodic orbits of type $(1, +, -)$ and $\gamma_k \to \gamma_\infty$. This completes the proof. ∎

Theorem 4.3. *Let (4.4) be an analytic monotone cyclic feedback system with $\Delta = -1$ in $\mathbf{R}^n_+$ which possesses a compact attractor $A \subset \dot{R}^n_+$. Suppose that A contains a single equilibrium x_* and that $Df(x_*)$ satisfies (4.5) and has at least two eigenvalues with positive real part. Then (4.4) has at least one, but no more than a finite number of, nontrivial periodic orbits. Moreover, at least one of these is orbitally asymptotically stable.*

Proof. By Theorem 4.1, there exists at least one nonconstant periodic orbit. By Theorem 4.2 one of these periodic orbits is orbitally stable. If every nonconstant periodic orbit is isolated in the sense that there is a neighborhood of it containing no point of any other periodic orbit, then the number of periodic orbits is finite in number. Indeed, if there exists an infinite number of periodic orbits, then they all belong to A, and furthermore, they are nested in the sense that either $\Pi^i x_* < \gamma^i < \tilde{\gamma}^i$ or $\Pi^i x_* < \tilde{\gamma}^i < \gamma^i$, where γ, $\tilde{\gamma}$ are two periodic orbits and $\gamma^i = \Pi^i \gamma$. Hence we may choose a totally ordered sequence of distinct orbits: γ_n with either $\gamma_n < \gamma_{n+1}$ or $\gamma_{n+1} < \gamma_n$, $n = 1, 2, \ldots$. Corollary 3.7 implies that the set Ω of limit points of the γ_n is either x_*, a nonconstant periodic orbit, or x_* together with a nonempty set of homoclinic orbits. We have ruled out the existence of homoclinic orbits by assuming that (4.5) holds and Ω cannot be a periodic orbit if we assume (for the moment) that all periodic orbits are isolated. The only possibility, then, is that $\Omega = x_*$. In this last case, x_* is not hyperbolic and since (4.5) holds, $Df(x_*)$ must have two purely imaginary eigenvalues and dim $W^c = 2$, where W^c is the center-manifold of x_*, from the theory in Section 2. Now by standard methods in bifurcation theory (see, e.g., Ref. 44), one can construct an analytic, scalar-valued, bifurcation (amplitude) equation, the zeros of which are in one-to-one correspondence with the periodic solutions of (4.4) in a neighborhood of x_*. As there are periodic solutions accumulating at x_*, analyticity forces this function to vanish identically near zero, implying the existence of a one-parameter family of periodic orbits bifurcating from x_*. This violates our (tentative) hypothesis that all periodic orbits are isolated. Thus the set of periodic orbits is finite under the hypothesis that every periodic orbit is isolated.

Furthermore, an orbitally stable periodic orbit γ which is isolated must be orbitally asymptotically stable. Indeed, let U be a neighborhood of γ whose closure contains no point of any other periodic orbit including x_*. Let $V \subset U$ be a neighborhood of γ such that if $x_0 \in V$, then $\gamma^+(x_0) \subset U$. Then $\omega(x_0) \subset \bar{U} \cap A$ must be γ, for each $x_0 \in V$. Thus γ is orbitally asymptotically stable.

The proof will be complete provided we show that each periodic orbit is isolated.

Fix i and let $T^i = \{x \in \mathbf{R}^n_+ : x^i = x^i_* \text{ and } f^i(x^i_*, x^{i-1}) > 0\}$. Every periodic orbit γ satisfies $\Pi^i x_* \in (\Pi^i \gamma)_{\text{int}}$ by Remark 3.1 and γ meets T^i in exactly one point, which belongs to $T^i \cap A$. Suppose that γ_0 is a nonisolated periodic orbit. By Theorem 3.3, $\gamma_0 \cap T^i$ is a nonisolated fixed point of a Poincaré map defined as in the proof of Theorem 3.3. Since 1 is a simple eigenvalue of the linearized Poincaré map at $\gamma_0 \cap T^i$, by the theory in Section 2, and since $\gamma_0 \cap T^i$ is a nonisolated fixed point and the Poincaré map is analytic, it follows from a standard Lyapunov–Schmidt argument that $\gamma_0 \cap T^i$ belongs to an analytic arc of fixed points of the Poincaré map. Each point of the arc represents a distinct periodic orbit. By a Zorn's lemma argument, this local arc of fixed points can be extended to a maximal analytical arc Γ in $T^i \cap A$. That is, Γ is not a proper subset of any other analytic arc of fixed points. There are two alternatives. First, $\Gamma \cong S^1$ closes on itself. But then the union of periodic orbits through P span a two-dimensional torus, τ. If y and z belong to τ, $y \neq z$, then $N(y-z)$ is defined since each point belongs to a periodic orbit. Thus $\Pi^i y \neq \Pi^i z$. Hence $\Pi^i : \tau \to \mathbf{R}^2$ is a homeomorphism of a torus onto a set in R^2, a contradiction. Thus Γ must be a Jordan (nonintersecting) arc of distinct nontrivial periodic orbits. Let $\xi : (0, 1) \to \Gamma$ be a parametrization of Γ. Now the family of periodic orbits $\{\gamma_{\xi(s)}\}_{s \in (0,1)}$ through the points of $\xi(s)$, $0 < s < 1$, are totally ordered in the sense defined in Corollary 3.7. That is, if $0 < s < s' < 1$, then either $\gamma_{\xi(s)} < \gamma_{\xi(s')}$ or $\gamma_{\xi(s')} < \gamma_{\xi(s)}$. It follows that $\xi^{i-1}(s)$ is one-to-one on $(0, 1)$ into $\mathbf{R}$. By reparametrizing Γ if necessary, we may assume that $\xi^{i-1}(s)$ is monotone increasing with s, i.e., $\gamma_{\xi(s)} < \gamma_{\xi(s')}$ if $0 < s < s' < 1$. Let $\{s_m\}$ be an increasing sequence satisfying $s_m \to 1$ and let $\gamma_m = \gamma_{\xi(s_m)}$. By Corollary 3.7, with $B = A$, the set of limit points Ω of $\{\gamma_m\}$ consists of either x_*, a nontrivial periodic orbit, or x_* together with a nonempty set of homoclinic orbits. The first and last alternatives cannot occur since the γ_m are increasing in the sense of $<$. In fact, there are no homoclinic orbits. Thus Ω is a nontrivial periodic orbit γ_1. Moreover, γ_1 is independent of the sequence $\{s_n\}$ so that $\gamma_{\xi(s)} \to \gamma_1$ as $s \to 1$ in the sense of the Hausdorff metric. But this contradicts the maximality of Γ and this contradiction completes the argument that every periodic orbit is isolated. ∎

In order to apply Theorem 4.1 to Eqs. (4.1) assuming (NF), observe that

$$\begin{aligned} B \equiv {} & [0, (\alpha^1)^{-1} f(0)] \times [0, \beta^2(\alpha^1\alpha^2)^{-1} f(0)] \times \cdots \\ & \times [0, \beta^2 \cdots \beta^n(\alpha^1\alpha^2 \cdots \alpha^n)^{-1} f(0)] \end{aligned} \tag{4.9}$$

is positively invariant for (4.1). Also, one can show (see, e.g., Ref. 36) that B attracts all orbits beginning in $\mathbf{R}^n_+$. In particular, all forward orbits are bounded. B also contains a unique equilibrium, x_*. Depending on the parameters α^i, β^i and the magnitude of f' at the equilibrium (see Refs. 36 and 43 for precise conditions), $Df(x_*)$ has at least two eigenvalues with positive real part. Hence, Theorem 4.1 implies that all orbits beginning in a relatively open subset of $\mathbf{R}^n_+$ are asymptotic to a nontrivial closed orbit. If, in addition, x_* is hyperbolic, then all orbits not on the stable manifold of x_* are asymptotic to a nontrivial closed orbit. For three-dimensional systems, this last result can be obtained from special results available for three-dimensional competitive systems (see Ref. 35).

The application of Theorem 4.1 to (4.2) follows similar arguments.

It is not immediately clear that Theorem 4.1 applies to (4.3). In fact, it generally does not apply in case the number of genes G is even [recall in (4.3), $G=3$]. In the case of even G, it is shown in Ref. 36 that a change of variables can be applied to (4.3), resulting in a cooperative system. In this case, as for (4.1) when (PF) holds, "almost all" solutions are asymptotic to a critical point (there can be several stable ones).

Theorem 4.1 does apply to (4.3) when G is odd. We carry out the details only for the case $G=3$; following this, the general case will be transparent. One first establishes that (4.3) possesses a compact attractor, B, in $\mathbf{R}^{p+l+m}_+$ in the same way as for (4.1) (see Ref. 36):

$$(y, z, w) \in B \equiv B_1 \times B_2 \times B_3$$

in which B_1 is B in (4.9) with $f=f^1$ and B_2 and B_3 are defined in the obvious way. Hence, one need only examine the behavior of solutions of (4.3) in B. For simplicity of notation, we write $B_2 = \prod_{j=1}^{l} [0, b^j]$ and define new variables

$$\bar{y}^i = y^i$$

$$\bar{z}^j = b^j - z^j$$

$$\bar{w}^k = w^k$$

Note that this transformation maps B onto itself. The equations satisfied by the new variables are identical to (4.3) except that $f^2(y^p) \to f^2(0) - f^2(\bar{y}^p)$ and $f^3(z^l) \to f^3(b^l - \bar{z}^l)$. Thus, the new equations in B define a monotone cyclic feedback system for which (4.6) holds and for which $\delta^1 = -1$ and $\delta^i = +1$ for $i \neq 1$. There is a unique critical point x_* of this system in B and sufficient for $Df(x_*)$ to have at least two eigenvalues with positive real part are known (see, Ref. e.g., Ref. 36). Theorem 4.1 applies to obtain a result identical to that obtained for (4.1).

If f in (4.1) and (4.2) or f^1, f^2, f^3 in (4.3) are analytic, then Theorem 4.3 gives sufficient conditions for each system to have a nonempty finite set of periodic solutions, at least one of which is orbitally asymptotically stable. The hypothesis (4.5) holds in these examples as noted in Remark 4.1. It is easy to see that each system possesses a compact attractor in $\dot{R}^n_+$ by noting that points on the boundary of $\mathbf{R}^n_+$ immediately enter $\dot{\mathbf{R}}^n_+$.

It is biologically reasonable to include time delays in the first terms on the right-hand side of (4.1) (or 4.3), particularly in y^p in the first equation. Many authors have considered the effect of time delays in the models (4.1) and (4.3) [1, 2, 4, 7, 25–28, 36]. For a special form of delay, considered by MacDonald in Ref. 25, Theorem 4.1 gives useful information. Replace y^p in the first equation in (4.1) by

$$\int_0^\infty y^p(t-u)\, G_a^q(u)\, du \tag{4.10}$$

where the kernel, G_a^q, is

$$G_a^q(u) = \frac{a^{q+1}u^q}{q!} e^{-au}, \qquad a > 0, \qquad q \in \{0, 1, 2,...\}.$$

Since $dG_a^q/du = a[G_a^{q-1} - G_a^q]$, $q \geqslant 1$, it is natural to introduce the new variables

$$y^{p+j}(t) = \int_0^\infty y^p(t-u)\, G_a^{j-1}(u)\, du, \qquad j = 1,..., q+1$$

and observe that

$$\begin{aligned} \dot{y}^{p+j}(t) &= \frac{d}{dt}\int_{-\infty}^t y^p(u)\, G_a^{j-1}(t-u)\, du \\ &= a(y^{p+j-1} - y^{p+j}), \qquad j = 1,..., q+1. \end{aligned} \tag{4.11}$$

In terms of the variables $y^1,..., y^{p+q+1}$, Eq. (4.1) with (4.10) takes the same form as (4.1) with $f(y^p)$ becoming $f(y^{p+q+1})$.

Of course, (4.1) with (4.10) is not equivalent to the enlarged system of Eqs. (4.1) and (4.11). They do, however, share the same set of bounded solutions on $\mathbf{R}$. That is, if $y\colon \mathbf{R} \to \mathbf{R}^p$ is a bounded solution of (4.1) with (4.10) then $\hat{y} = (y, y^{p+1},..., y^{p+q+1})$ is a bounded solution of (4.1) and (4.11), and vice versa. In particular, they share the same periodic solutions. Hence, Theorem 4.1 can be used to prove the existence of periodic solutions of (4.1) with (4.10). Macdonald [25] has obtained sufficient conditions for the critical point of (4.1) and (4.11) to have a pair of unstable eigenvalues for a particular nonlinearity f of Michaelis–Menten form. In this case, Theorem 4.1 and earlier arguments imply that (4.1) with (4.10) has a nonconstant periodic orbit.

Certain nth-order scalar differential equations are equivalent to monotone cyclic feedback systems. Consider the equation

$$x^{(n)} + f(x, x^{(n-1)}) = 0 \tag{4.12}$$

where $f: \mathbf{R}^2 \to \mathbf{R}$ is a smooth function satisfying

$$\frac{\partial f(x, y)}{\partial x} > 0 \qquad \text{for all } (x, y).$$

If we let

$$x^i = x^{(n-i)}, \qquad 1 \leqslant i \leqslant n,$$

then (4.12) is equivalent to the monotone cyclic feedback system

$$\begin{aligned} \dot{x}^1 &= -f(x^n, x^1) \\ \dot{x}^i &= x^{i-1}, \qquad 2 \leqslant i \leqslant n \end{aligned} \tag{4.13}$$

It can be checked that (4.13) has a unique critical point x_* in $\mathbf{R}^n$ if $f(-\infty, 0) < 0$, and $f(\infty, 0) > 0$, so Theorem 4.1 (with $\mathbf{R}^n$ replacing $\mathbf{R}^n_+$) can be applied to bounded orbits of this system. An interesting special case of (4.12) is given by

$$x^{(n)} + f(x) = 0 \tag{4.14}$$

where $f'(x) > 0$ for all x.

However, (4.14) cannot have interesting stable solutions if $n \geqslant 3$. It is easy to see that if $n \geqslant 3$, then any critical point possesses eigenvalues with positive real parts. It is also the case that any periodic orbit of (4.14) has characteristic multipliers with modulus exceeding unity. This results from two facts, (a) the divergence of the vector field is zero and hence the product of the moduli of the multipliers equals unity and (b) no multiplier has multiplicity exceeding two. The same arguments apply to (4.12) if one assumes $\partial f(x, y)/\partial y \leqslant 0$, namely, that any steady state or periodic orbit must be unstable in the linear approximation. We note that if $\partial f/\partial y < 0$ and $n = 3$, Leonov [23] has shown that (4.12) cannot have any nonconstant periodic orbits.

In order to obtain the existence of nontrivial closed orbits of (4.12) by Theorem 4.1, it is necessary to show that (4.12) possesses nontrivial bounded (for $t \geqslant 0$) solutions. This is a nontrivial task. The interested reader is referred to the book by Reissig *et al.* [32]. Unfortunately, the results in Ref. 32 do not seem to apply to (4.12). Indeed, arguing as in Remark 4.4 shows that if $\partial f/\partial x > 0$ and $\partial f/\partial y \leqslant 0$ in $\mathbf{R}^2$, then almost every orbit of the system is unbounded as $t \to \infty$.

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