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THE EXISTENCE OF AN EQUILIBRIUM FOR PERMANENT SYSTEMS

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ABSTRACT. The criterion of permanence for biological systems requires that there exist a compact attractor for the interior of the positive cone X lying in $\operatorname{int} X$. It is shown here that for several models permanence implies the existence of an equilibrium point in $\operatorname{int} X$ corresponding to a stationary coexistence state.

1. Introduction. The criterion of permanence for biological systems is a condition ensuring the long-term survival of all species. Sufficient conditions for permanence have been given for a wide variety of models, see, for example, [**3, 4, 5, 7, 8, 10, 11, 12, 13**]. To illustrate the question to be tackled here, consider a model based on a system of autonomous ordinary differential equations

$$\dot{x}_i = x_i f_i(x), \qquad i = 1, \dots, n, \tag{1}$$

on the positive cone $\mathbf{R}^n_+$, where $x = (x_1, \dots, x_n)$ and conditions ensuring the global existence and uniqueness of solutions in forward time are imposed. The system (1) is said to be *permanent* if there exist $m, M \in (0, \infty)$ such that, given any $x \in \operatorname{int} \mathbf{R}^n_+$, there is a t_x such that

$$m \le x_i(t) \le M, \qquad i = 1, \dots, n, t \ge t_x.$$

From a biological point of view, it is reasonable to expect that if permanence holds, there will be a stationary coexistence state in $\operatorname{int} \mathbf{R}^n_+$. If such a state does exist, a natural necessary condition for permanence follows. An analogous question may be asked for the system of difference equations

$$x_i' = x_i f_i(x), \qquad i = 1, \dots, n, \tag{2}$$

where x_i' denotes the value of x_i at the next generation. As has been noted, for example, in [**8**] and [**10**], the question for both these systems has an affirmative answer. The methods of proof have often been based on rather deep results concerning the existence of fixed points of abstract dynamical systems. Here it is shown that a very simple proof may be supplied. In addition, analogous results are established for systems of reaction-diffusion equations and of autonomous differential-delay equations, where the phase spaces are not locally compact. The proofs are based on a direct appeal to the asymptotic fixed point theorems of Schauder and Horn and are extremely straightforward.

A few preliminary remarks may help to clarify the broad strategy for those readers unfamiliar with this general area. Consider the continuous map $A : \mathbf{R}_+^n \to \mathbf{R}_+^n$ generated by (2), and suppose there is a compact set $M \subset \operatorname{int} \mathbf{R}_+^n$ which is invariant in forward time and which is reached by all orbits with initial values in $\operatorname{int} \mathbf{R}_+^n$. If M is convex, a straight application of the Brouwer fixed point theorem yields a fixed point in M. However, in the present context, it is difficult to construct an M that is both convex and forward invariant, although either condition on its own is easily fulfilled. Broadly, the use of an asymptotic fixed point theorem weakens the requirement of forward invariance and provides a way of avoiding this difficulty.

In the next section the dynamical system background is briefly outlined, and the fixed point theorems stated. In §3 applications are given to situations where the flow immediately smooths orbits, while in §4 it is shown that it is enough if orbits are only "eventually" smoothed. In §5 the analogous question for set-valued maps is raised.

2. Dynamical systems. Let (X, d) be a metric space. So that discrete and continuous dynamical systems may be treated in one framework, $\mathbf{D}_+$ will denote either the nonnegative integers $\mathbf{Z}_+$ or the nonnegative reals $\mathbf{R}_+$ as appropriate. With the terminology of [**2**], consider the semi-dynamical system $(X, \mathbf{D}_+, \pi)$, and let $\gamma^+(x)$ denote the semi-orbit through x:

$$\gamma^+(x) = \{y : y = \pi(x,t) \text{ for some } t \in \mathbf{D}_+\}.$$

For a subset $U \subset X$, $\gamma^+(U)$ is defined by taking unions. U is said to be *forward invariant* if $\gamma^+(U) \subset U$ and *absorbing* for V if it is forward invariant and $\gamma^+(x) \cap U \neq \varnothing$ for all $x \in V$. x is an *equilibrium point* if $\pi(x,t) = x$ $(t \geq 0)$. A semi-orbit $\gamma^+(x) = \gamma$, say, is said to be *periodic* with period T if $\pi(y,T) = y$ for all $y \in \gamma$.

The proof of the first of the following two standard results may be obtained by a minor modification of the proof of Lemma 2.1 of [**11**] and is omitted. The second is given in [**2**, p. 81].

LEMMA 1. *Let Y be a subspace of X, and let U, M_0 be subsets of Y such that $\gamma^+(U)$, $\gamma^+(\overline{M}_0) \subset Y$. Assume that M_0 is open in Y, and that U, $\overline{M}_0$ are compact. Then, with $M = \gamma^+(\overline{M}_0)$, the following hold.*

(i) *If $\gamma^+(x) \cap M_0 \neq \varnothing$ for all $x \in \overline{M}_0$, M is compact and forward invariant.*

(ii) *If, in addition, $\gamma^+(x) \cap M_0 \neq \varnothing$ for all $x \in U$, there exists T such that, given any $x \in U$, $\pi(x,t) \in M$ for all $t \geq T$.*

LEMMA 2. *Suppose that $M \subset X$ is compact and forward invariant. Assume that there is a sequence $\{T_n\} \subset \mathbf{R}_+$, with $\lim_{n\to\infty} T_n = 0$, and a sequence $\{\gamma_n\}$ of periodic orbits with periods T_n, respectively, in M. Then M contains an equilibrium point.*

The two asymptotic fixed point theorems to be used are as follows. For a proof of the first see [**14**, p. 725]. The second is a weak version of a theorem of Horn [**9**] which is sufficient for the present purpose. B denotes a Banach space. An operator $A : U \subset B \to B$ is said to be *completely continuous* if it is continuous and maps bounded sets into relatively compact sets.

THEOREM 3. (Schauder). *Let $U \subset B$ be nonempty bounded, open and convex, and suppose that $A : B \to B$ is completely continuous. Assume that, for some fixed prime $p \geq 2$, $A^k\overline{U} \subset U$ for $k = p$, $p+1$. Then A has a fixed point in U.*

THEOREM 4. (Horn). *Let $U_0 \subset U_1 \subset U_2 \subset B$ be convex with U_0 and U_2 compact, and U_1 open in U_2. Let $A : U_2 \to B$ be continuous, and assume that $A^kU_1 \subset U_2$ for $k \in \mathbf{Z}^+$. Suppose also that there exists an integer $m > 0$ such that $A^kU_1 \subset U_0$ for $k \geq m$. Then A has a fixed point in U_0.*

3. Applications of the Schauder Theorem. It will first be shown how the existence of an interior equilibrium may be established for the system of differential equations (1) and difference equations (2). For a discussion of permanence in these cases, see, for example, [**8**, **11**] and [**5**, **7**, **10**] respectively. The situation for systems of reaction-diffusion equations is then considered.

THEOREM 5. *Suppose that permanence holds for the system of difference equations* (2) *or the system of differential equations* (1). *Then, in each case, respectively, there exists an equilibrium point in* $\operatorname{int} \mathbf{R}_+^n$.

PROOF. Consider first the difference equation case, and let A denote the associated operator. Let M_0 be the n-dimensional cube

$$\{x : m < x_i < M \text{ for } i = 1, \dots, n\}.$$

By Lemma 1(i), $M = \gamma^+(\overline{M}_0)$ is compact and contained in $\operatorname{int} \mathbf{R}_+^n$. It is also absorbing for $\operatorname{int} \mathbf{R}_+^n$. Clearly M may be enclosed in an open cube U, say, with $U \subset \operatorname{int} \mathbf{R}_+^n$. By Lemma 1(ii), there is a $k_0 \in \mathbf{Z}^+$ such that $A^k\overline{U} \subset M$ for $k \geq k_0$. The result follows from Theorem 3 on choosing any prime $p \geq k_0$.

For the differential equation case (1), choose any $t > 0$ and define A by setting $Ax = \pi(x, t)$. A very similar argument yields a fixed point of A (which gives, of course, a periodic orbit of period t). As this holds for every $t > 0$, the result follows from Lemma 2. $\square$

The key feature of the above proof is that $\pi(x, t)$ is completely continuous for each $t > 0$. If this condition holds, the proof will extend readily to situations in which the phase space is not locally compact. It is well known, see [**6**], for example, that this condition holds for a wide range of systems of reaction-diffusion equations on an appropriate Banach space. Hence, if permanence can be proved, the existence of a (stationary) equilibrium state will follow. This is a trivial observation if the equations themselves are spatially independent, as it follows directly from the ordinary differential equation result above, but is much less obvious if the space variable enters into the equations. In fact, so far as the author is aware, permanence has only been considered for systems of reaction-diffusion equations in the spatially independent case, see [**13**]. We shall not, therefore, further pursue this point here but shall turn to a case where the above condition on π is not satisfied for all $t > 0$.

4. Applications of Horn's Theorem to differential-delay systems. In [**3**] permanence has been established for a class of differential-delay systems which occur in applications, and it will be shown that, analogously, an interior equilibrium point exists. However, it appears that the method of the previous section is not applicable. To illustrate the difficulty, consider, for example, the system

$$\dot{x}_i(t) = x_i(t)\left[a_i + \int_{t-\tau}^{t} k_i(s-t) f_i(x(s))\, ds\right],$$

for $i = 1, \dots, n$, where τ is a positive finite number. Let B be the Banach space $C([-\tau, 0], \mathbf{R}_+^n)$ with the sup norm $\| \cdot \|$, and take the phase space X to be the positive cone of B with the usual ordering. It is clear that, under reasonable conditions on the k_i and f_i, orbits lying in a ball in X will, after time τ, lie in a ball in $C^1([-\tau, 0], \mathbf{R}_+^n)$. It follows that the associated flow $\pi(\cdot, t)$ is compact for $t \geq \tau$, but *not* necessarily for all $t > 0$. To get around this problem, Horn's asymptotic fixed point theorem will be used.

Let S be the subset of X consisting of those x with $x_i(0) = 0$ for some i, where x_i is the i-th component of x. Let $B(r)$ be the intersection of the open ball, with center the origin and radius r, with X, and let $\mathrm{Lip}\,(L)$ be the set of functions in X satisfying a Lipschitz condition with constant L.

Some boundedness conditions on solutions are clearly needed. In view of the above discussion, the following represent, then, a typical set of conditions on a system of differential-delay equations for which permanence holds.

(i) Ultimate uniform boundedness with bound b. There exists b such that, given $\alpha > 0$, there is a t_α such that $\pi(x, t) \in \overline{B}(b)$ if $x \in \overline{B}(\alpha)$ and $t \geq t_\alpha$.

(ii) Uniform boundedness. Given $\beta > 0$, there exists $C(\beta)$ such that $\pi(x, t) \in \overline{B}(C(\beta))$ if $x \in \overline{B}(\beta)$ and $t \geq 0$.

(iii) Permanence. There exists $m > 0$ such that, for any $x \in \operatorname{int} X$, there is a t_x such that $[\pi(x,t)]_i(0) \geq m$ for $t \geq t_x$ and all i, where this denotes the value of the i-th component at 0.

(iv) Given $\alpha > 0$, there exists $L(\alpha)$ such that if $x \in \overline{B}(\alpha+1) \cap \operatorname{Lip}(L(\alpha))$, then $\pi(x,t) \in \operatorname{Lip}(L(\alpha))$ for $t \geq 0$.

THEOREM 6. *Under conditions* (i)–(iv), *the delay system has an equilibrium state consisting of a constant solution in* $\operatorname{int} \mathbf{R}_+^n$.

PROOF. By (ii) there exists c such that if $\|u\| \leq b+1$, then $\|\pi(x,t)\| < c$ $(t > 0)$. In (iv) take $\alpha = b+1$ and put $L = L(b+1)$. Define M_0, $U_2 \subset X$ as follows:

$$U_2 = \{x : \|x\| \leq c,\ x \in \operatorname{Lip}(L)\},$$
$$M_0 = \{x : \|x\| < b+1, x_i(0) > m/2 \text{ for all } i\} \cap U_2.$$

Clearly U_2 is compact and convex, M_0 is open in U_2, and $\overline{M}_0$ (its closure in U_2) is compact. By (i), if $x \in M_0$, $\pi(x,t) \in U_2$ $(t \geq 0)$, and by (i), (iii) and (iv), there is a t_x such that $\pi(x,t_x) \in M_0$. By Lemma 1, $\gamma^+(\overline{M}_0)$ is compact and does not intersect S. Thus, there is an $m_1 \in (0,m)$ such that if $x \in M_0$, then $[\pi(x,t)]_i(0) > m_1 (t \geq 0)$. Put

$$U_0 = \{x : \|x\| \leq b,\ x_i(0) \geq m_1 \text{ for all } i\} \cap U_2,$$
$$U_1 = \{x : \|x\| < b+1,\ x_i(0) > m_1/2 \text{ for all } i\} \cap U_2.$$

U_1 is open in U_2 and its closure $\overline{U}_1$ in U_2 is compact. Thus, from Lemma 1, there is a T_1 such that if $x \in \overline{U}_1$, then $\pi(x,t) \in M_0$ for some $t \leq T_1$. It follows from the definition of m_1 that $[\pi(x,t)]_i(0) > m_1/2$ for $t \geq T_1$. By (i) there is a T_2 such that if $x \in \overline{U}_1$, $\|\pi(x,t)\| < b+1$ for $t \geq T_2$. Therefore, $\pi(x,t) \in U_0$ for $t \geq T := T_1 + T_2$.

Take now any fixed $t > 0$ and put $A = \pi(\cdot, t)$. Clearly, $A^k U_1 \subset U_2$ for all k and, for $kt > T$, $A^k U_1 \subset U_0$. From Theorem 4, A has a fixed point in U_0. Since t is arbitrary, the assertion of the theorem follows from Lemma 2. □

5. Differential inclusions. In view of the difficulty of specifying the model precisely in biological applications, it is natural to inquire whether the permanence question can be tackled for a system of differential inclusions [**1**],

$$\dot{x}_i \in F_i(x), \qquad i = 1, \dots, n,$$

where the F_i are set valued maps. A preliminary discussion of this problem has been given in [**12**], using a set valued dynamical system, and conditions established for permanence. In outline, the technique is to define π as a map of $X \times \mathbf{R}_+$ into the set of nonempty subsets of X. The usual semigroup property is required of π, and it is assumed that π is upper semicontinuous and compact valued. The system is said to be permanent if there exists m, $M \in (0, \infty)$ such that, given $x \in \operatorname{int} \mathbf{R}_+^n$, there is a t_x such that $\pi(x, t) \subset \overline{M}_0$ where M_0 is the cube $\{x : m < x_i < M \text{ for } i = 1, \dots, n\}$.

It seems likely that, by analogy with the cases treated previously, permanence will imply the existence of an equilibrium in $\operatorname{int} \mathbf{R}_+^n$, that is, a point x such that $x \in \pi(x, t)$ for $t \geq 0$. Such a result would follow if a theorem for set valued maps analogous to the Asymptotic Schauder Fixed Point Theorem 3 existed. However, it is unknown to the author whether or not this is the case, and the question of the existence of an equilibrium state appears still open.

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