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REPELLERS IN REACTION-DIFFUSION SYSTEMS

V. HUTSON AND W. MORAN

ABSTRACT. A technique for discovering when an invariant set for a reaction-diffusion system is a repeller in a certain strong sense is studied. The criterion is based on a weakening of the standard requirements for Liapunov functionals for repellers. The analysis is motivated by the coexistence question for several interacting species in mathematical biology.

1. Introduction. In biological applications, see [**4**], the following initial/boundary value problem for a system of reaction-diffusion equations in $D \times \mathbf{R}_+$ is often encountered:

$$\partial u_i/\partial t = \mu_i \Delta u_i + u_i f_i(u), \tag{1.1a}$$

$$\partial u_i/\partial \nu = 0 \quad (\text{on } \partial D \times \mathbf{R}_+), \tag{1.1b}$$

$$u(x,0) = u_0(x) \quad (x \in \overline{D}), \tag{1.1c}$$

where $1 \leq i \leq n$ and $u = (u_1, \ldots, u_n)$. Here, D is a bounded domain in $\mathbf{R}^m$ with smooth boundary, $\partial/\partial\nu$ denotes differentiation along the normal to ∂D and Δ is the Laplacian. The function u_i is the density of the i^{th} population, and the boundary condition (1.1b) requires that there should be no migration across ∂D. Only non-negative solutions are of interest, and it should be noted that from the form of the equations, each of the sets $u_i(x) = 0 (x \in \overline{D})$ is forward invariant.

The problem considered here, that of obtaining criteria for the long term survival of the species, is one of the most fundamental from the point of view of applications. However, precisely how 'survival' ought to be interpreted is not clear, and indeed for the much simpler model based on the corresponding ordinary differential equations, there have been a number of definitions proposed in the literature. The definition that will be used here is as follows: the system (1.1) will be said to be *permanently coexistent* if and only if there exists an $\varepsilon > 0$ such that,

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for each continuous u_0 with no component identically zero, there is a $t_0(u_0)$ such that

$$\int_{\overline{D}} u_i(x,t)\,dx \geq \varepsilon \quad (1 \leq i \leq n, t \geq t_0(u_0))\,.$$

Permanent coexistence is thus global in the sense that it ensures that the average species densities are eventually repelled from zero in a uniform manner; that is, they have asymptotically a certain minimum value which is independent of the initial conditions. However there is otherwise no restriction on the asymptotic behavior of the system. This is of particular importance if the definition is to be biologically realistic, for it is well known that even quite simple kinetic systems for three species may have complicated asymptotic behaviour such as a strange attractor [**2**], but there is no reason why this should rule out survival, so long as orbits are repelled from the boundary (representing extinction). For models based on ordinary differential equations, further discussion and references to the biological background may be found in [**9**].

From a mathematical point of view, this definition raises a point of some interest, for permanent coexistence may be regarded as a global stability criterion, but with the requirement that orbits should be (uniformly) repelled from a certain invariant set (the boundary in this case). This is in contrast with the more usual approach to stability where the object is to show that a certain set is an attractor. In fact, except in very simple systems of the form (1.1), it is likely to be extremely hard to locate the attractor, whereas the technique which is described here will allow us to establish stability in the above sense in a relatively wide range of applications.

A possible way of tackling these questions is to reverse the usual technique, and to search for a Liapunov functional vanishing on the set and increasing along orbits. However, unless the number of species is low (usually not greater than two) or the system is quite special, it will probably be difficult to find such a functional. Our approach has its genesis in a method for ordinary differential equations, see [**13, 6, 8**], where the requirements on the Liapunov functional are significantly weakened. The basic tool is a result on dynamical systems on a compact metric space, the compactness for the orbits of (1.1) being supplied from an *a priori* derivative bound. In §2 the precise assumptions concerning (1.1) are described and the *a priori* bound established. §3 contains the central dynamical systems result, and §4 discusses its application to the reaction-diffusion system. Finally, in §5 a specific problem arising in mathematical biology is tackled by this method.

2. Preliminaries. For Ω a nice domain in $\mathbf{R}^i$, $C(\Omega, \mathbf{R}^j)$, respectively $C^k(\Omega, \mathbf{R}^j)$, will denote the sets of continuous, respectively k times continuously differentiable, functions $\Omega \to \mathbf{R}^j$. When $\Omega = \overline{D}$, the usual norms on the corresponding Banach spaces will be denoted by $\|\cdot\|$, respectively $\|\cdot\|_{C^k}$. The following assumptions will be imposed throughout on the system (1.1).

(H1). D is a bounded open domain in $\mathbf{R}^m$ with C^2 boundary. For each i, $f_i \in C^2(R^n, R)$, and $\mu_i > 0$.

It is reasonable to assume that in realistic biological models, intraspecific competition operates. As a consequence, it will usually be possible to show by the methods of [**14,** Chap. 14] not only that there is an *a priori* L^∞ bound on solutions (from which existence and uniqueness of classical solutions will follow), but also that eventually every solution will enter and remain in a fixed bounded L^∞ neighbourhood of the origin. So far as the question of permanent coexistence is concerned, it is clearly enough to restrict attention to this neighbourhood. For $Y \subset \mathbf{R}^n_+$, let then

$$X_0 = \{u \in C(\overline{D}, \mathbf{R}^n) : u(x) \in Y (x \in \overline{D})\},$$
$$S_0 = \{u \in X_0 : \text{for some } i,\ u_i(x) = 0 (x \in \overline{D})\},$$

and assume the following.

(H2). For $u_0 \in C(\overline{D}, \mathbf{R}^n_+)$, global existence and uniqueness of classical solutions hold. Also there is a compact neighbourhood Y of the origin 0 in $\mathbf{R}^n_+$ such that X_0 is forward invariant, and for each u_0, there is a $t_0(u_0)$ such that the corresponding solution $u(\cdot, t) \in X_0$ for $t \geq t_0(u_0)$.

The following two lemmas will be needed in applying the dynamical systems result to (1.1). The first, which supplies the required compactness, seems well known, but a proof is not readily accessible and is sketched below.

LEMMA 2.1. *Let* (H1) *and* (H2) *hold. Then there exists* $m_0 < \infty$ *such that, for all* $u_0 \in X_0$, *solutions satisfy*

$$\|u(\cdot, t)\|_{C^1} \leq m_0 \quad (t \geq 1). \tag{2.1}$$

PROOF. With $v = u_i$, $\mu = \mu_i$ in turn, each equation may be written in the form

$$\frac{\partial v}{\partial t} - (\mu\Delta - a)v = g(x,t), \tag{2.2}$$

where

$$g(x,t) = au_i(x,t) + u_i(x,t)f_i(u(x,t)),$$

and $v(x,0) = v_0$. It is clearly enough to prove that, given m_1, the analogue of (2.1) holds for all v such that $\|v_0\| \leq m_1$. In view of (H2), it may be assumed without loss of generality that $v_0 \in C^2(\overline{D}, \mathbf{R})$, for otherwise the initial value problem starting at $t = \frac{1}{2}$ may be considered. Also, there is an m_2 such that $\|g(\cdot,t)\| \leq m_2 (t \geq 0)$.

By [**15,** p. 88], for some a, under homogeneous Neumann conditions $(\Delta - aI)$ generates an analytic semigroup in $E = L_p(\overline{D})$ for $p > 1$, and with $-A$ the associated operator, there is a $\delta > 0$ such that $Re\sigma(A) > \delta$ (where $\sigma(A)$ denotes the spectrum of A). Equation (2.2) may then be rewritten in an obvious notation as

$$\frac{dv}{dt} + Av = G,$$

with solution

$$v(t) = e^{-At}v_0 + \int_0^t e^{-A(t-s)}G(s)\,ds. \tag{2.3}$$

From [**5,** p. 26], for $\alpha > 0$,

$$\|A^\alpha e^{-At}\|_E \leq C(\alpha)t^{-\alpha}e^{-\delta t}, \tag{2.4}$$

where $\|\cdot\|_E$ is also used to denote the operator norm. Taking some $\alpha \in (0,1)$, applying A^α to (2.3), and taking norms, we obtain

$$\begin{aligned}\|A^\alpha v(t)\|_E &\leq \|A^\alpha e^{-A(t-s)}\|_E\|v_0\|_E + \int_0^t \|A^\alpha e^{-A(t-s)}\|_E\|G(s)\|_E\,ds \\ &\leq C(\alpha)(t^{-\alpha}e^{-\delta t}\|v_0\|_E \\ &\quad + \max_{0\leq s\leq t}\|G(s)\|_E \int_0^t (t-s)^{-\alpha}e^{-\delta(t-s)}\,ds),\end{aligned}$$

by (2.4). It follows from the bounds on v_0 and g that there is an m_3 such that

$$\|A^\alpha v(t)\|_E \le m_3 \quad (t \ge 1). \tag{2.5}$$

From the definition of the fractional space E^α [**5**, p. 29], and a standard imbedding theorem [**5**, p. 39], respectively,

$$\|A^\alpha v(t)\|_E = \|v(t)\|_{E^\alpha}, \tag{2.6}$$

$$\|v(t)\|_{C^\nu} \le k\|v(t)\|_{E^\alpha} \quad (0 \le \nu \le 2\alpha - m/p), \tag{2.7}$$

where k is independent of u. Taking $\alpha = 3/4, p = 2m, \nu = 1$, we obtain the result on combining (2.5), (2.6), and (2.7).

LEMMA 2.2. *If* (H1) *holds, given k, there is a $\beta > 0$ such that for all $v \in C^1(\overline{D}, \mathbf{R}_+)$ with $\|v\|_{C^1} \le k$,*

$$\|v\|_{L^1(\overline{D})} \ge \beta\|v\|^{m+1}.$$

PROOF. Since $\overline{D}$ has the cone property, there exist $\alpha,\ h > 0$ such that for each $x \in \overline{D}$ there is a cone K of height h, angle α, with vertex at x, which is contained in $\overline{D}$. Therefore, $K_0 \subset \overline{D}$, where K_0 is the intersection of K with the closed ball radius h, center x. Since $\overline{D}$ is compact, there is a point x_0 with $v(x_0) = \|v\|$. Take K_0 to have vertex x_0, and let $r = r(y)$ be the distance of y from x_0. By the Mean Value Theorem,

$$v(y) \ge v(x_0) - r(y)k \quad (y \in K_0, 0 \le r(y) \le R),$$

where $R = \min\{h, v(0)/k\}$. Hence, there is a $\beta_1 > 0$ such that

$$\|v\|_{L^1(\overline{D})} \ge \beta_1 \int_0^R [v(0) - rk]r^{m-1}\, dr$$

$$= \begin{cases} \beta_1[v(0)]^{m+1}/[m(m+1)k^m] & (h > v(0)/k), \\ \beta_1[v(0)/m - kh/(m+1)h^m] & (h \le v(0)/k). \end{cases}$$

When $h \le v(0)/k$, since $v(0) \le k$,

$$v(0)/m - kh/(m+1) \ge [v(0)]^{m+1}/[m(m+1)k^m],$$

and the result follows.

3. A result on dynamical systems. The basic theorem for the reaction-diffusion system (1.1) is deduced from a result for a dynamical system on a compact metric space. X_0 is of course not compact. However, by Lemma 2.1, initial data is smoothed 'uniformly quickly', and this suggests that instead of X_0, the phase space ought to be the closure of the collection of semi-orbits through X_0 after time $t = 1$.

For the standard theory (see, for example [**14**]) the solutions of (1.1) generate a dynamical system $(\pi, X_0, \mathbf{R}_+)$. Define $X = \pi(X_0, [1, \infty))$, $S = \pi(S_0, [1, \infty))$. In the sequel the dynamical system $(\pi, \overline{X}, \mathbf{R}_+)$ is used. We often write $\pi(u, t) = ut, \gamma^+(u)$ denotes the semi-orbit through u, and, for a subset $V \subset \overline{X}, \gamma^+(V) = \bigcup_{u \in V} \gamma^+(u)$. $\Omega(u)$ denotes the Ω-limit set of u, and $\Omega(v) = \bigcup_{v \in V} \Omega(u)$. A set M is said to be absorbing for V if, and only if, given any $u \in V$, there is a $t(u)$ such that $ut \in M$ for $t \geq t(u)$.

LEMMA 3.1. *Under* (H1) *and* (H2), *the following hold.*

(i) *If for some i and $x \in \overline{D}, u_i(x, 0) > 0$, then $u_i(x, t) > 0$ for all $x \in \overline{D}$ and $t > 0$.*

(ii) *$X, S, X \setminus S$ are forward invariant*

(iii) *$\overline{X}, \overline{S}, \overline{X} \setminus \overline{S}$ are forward invariant, and $\pi(\overline{X}, [1, \infty)) \subset X$.*

(iv) *$X \setminus S$ is dense in $\overline{X}$*

(v) *$\overline{S}$ is a compact subset of the compact metric space $\overline{X}$.*

PROOF. (i). This is a consequence of the maximum principle [**14**]. (ii). X_0 is forward invariant by (H2), S_0 from the form of the equations (1.1a). The assertion follows from the definition of X, S and (i). Since X, S are forward invariant, so are $\overline{X}, \overline{S}$. To show that $\overline{X} \setminus \overline{S}$ is forward invariant, first note that S_0 is closed and forward invariant. Also, if $u_0 t \in S_0$ for some $t > 0$, then $u_0 \in S_0$, for otherwise (i) is contradicted. Now $S \subset X \cap S_0$. On the other hand, if $u \in X$, there exist $u_0 \in X_0$, $t \geq 1$ such that $u_0 t = u$, and if $u \in S_0$, by a remark above, $u_0 \in S_0$. Hence, if $u \in X \cap S_0$, there is a $t \geq 1$ and $u_0 \in S_0$ such that $u_0 t = u$, whence $u \in S$ and $S \supset X \cap S_0$. Therefore, $S = X \cap S_0$, and $\overline{S} = \overline{X} \cap S_0$. Finally, if $u \in \overline{X} \setminus \overline{S}$ but $ut \in \overline{S}$ for some $t > 0$, then $u \in S_0$, and so $u \in \overline{X} \cap S_0 = \overline{S}$, a contradiction. (iv). S has empty interior, so $X \setminus S$ is dense in X and so in $\overline{X}$. (v). X is obviously relatively compact by Lemma 2.1 and the Arzela-Ascoli Theorem, so $\overline{X}$ is compact.

The result which follows weakens the requirements which would be imposed in a Liapunov function approach ensuring that $\overline{S}$ repels orbits in a strong sense. The function P may be regarded as a 'weak' Liapunov function in that the requirement that P be increasing along orbits is weakened in two ways: firstly, it is only required that the basic inequality holds on $\overline{\Omega(\overline{S})}$ rather than in a neighbourhood of the whole of $\overline{S}$; secondly, that it need only hold for some t rather than for all $t > 0$. Conditions (3.1) may reasonably be expected to ensure that orbits are repelled by $\overline{S}$; one of the main points of the theorem is that this is a uniform process in the sense that, after moving away from a neighbourhood of S, orbits may not return 'too close' to S.

THEOREM 3.2. *Assume that* (H1) *and* (H2) *hold. Let* $P : X\backslash S \to \mathbf{R}_+$ *be continuous, strictly positive and bounded. For* $u \in \overline{X}$ *define*

$$\alpha(t,u) = \liminf_{\substack{v \to u \\ v \in X\backslash S}} \frac{P(vt)}{P(v)},$$

and suppose that, for some $\tau > 0$,

$$\sup_{t \geq \tau} \alpha(t,u) > \begin{cases} 1 & \left(u \in \overline{\Omega(\overline{S})}\right), \\ 0 & (u \in \overline{S}). \end{cases} \tag{3.1b}$$

Then there is a compact set M *asbsorbing for* $\overline{X} \setminus \overline{S}$ *with* $d(M,\overline{S}) = \min_{u \in M} d(u,\overline{S}) > 0$.

PROOF. Observe first that $\alpha(t,\cdot)$ is lower semicontinuous. Also, for $t, t' > 0$ and $u \in \overline{X}$,

$$\begin{aligned} \alpha(t+t',u) &= \liminf_{\substack{v \to u \\ v \in X\backslash S}} \frac{P\left(v(t+t')\right)}{P(vt)} \cdot \frac{P(vt)}{P(v)} \\ &\geq \alpha(t,u) \cdot \alpha(t',ut), \end{aligned}$$

and therefore, for any $t_i > 0 (i = 0, 1, \dots, k)$,

$$\alpha(\sum_{i=0}^{i=k} t_i, u) \geq \alpha(t_0,u) \prod_{j=1}^{j=k} \alpha(t_j, u \sum_{i=0}^{i=j-1} t_i). \tag{3.2}$$

We claim that for any $T > 0$ and $u \in \overline{S}$, there is a $t_0 \geq T$ such that $\alpha(t_0,u) > 0$. By (3.1b) there is a $t_0 \geq \tau$ such that $\alpha(t_0,u) > 0$, and

$t_i \geq \tau$ may be chosen inductively so that $\alpha(t_i, u(t_0 + \ldots + t_{i-1})) > 0$. For some n, $t^* = t_0 + \ldots + t_n \geq T$, and by (3.2), $\alpha(t^*, u) > 0$. This proves the claim.

We next show that $\sup_{t \geq \tau} \alpha(t, u) > 1$ for any $u \in \overline{S}$. For $h > 0$, $t \geq \tau$, set

$$U(h, t) = \{u : \alpha(t, u) > 1 + h\},$$

and note that each $U(h, t)$ is open. From (3.1a), the $U(h, t)$ form an open cover of $\overline{\Omega(\overline{S})}$, so that by compactness there is a finite set $F \subset [\tau, \infty)$ and an $\overline{h} > 0$ such that

$$\overline{\Omega(\overline{S})} \subset \bigcup_{t \in F} U(h, t) = W,$$

say. Choose any $u \in \overline{S}$. By what was proved above, and from the definition of $\overline{\Omega(\overline{S})}$, there is a t_0 such that $ut \in W$ for $t \geq t_0$ and $\alpha(t_0, u) = \eta > 0$. Choose n such that $(1 + \overline{h})^n \eta \geq 1$. Take inductively $t_i \in F$ such that $ut_0 \in U(\overline{h}, t_1)$ and $u(t_0 + \ldots + t_{i-1}) \in U(\overline{h}, t_i)$. It follows from (3.2) that

$$\alpha(t_0 + \ldots + t_n, u) \geq (1 + \overline{h})^n \eta > 1,$$

which proves the assertion.

We may now repeat the argument of the previous paragraph and show that there is a finite set $G \subset [\tau, \infty)$ and an $h^* > 0$ such that

$$\overline{S} \subset \bigcup_{t \in G} U(h^*, t) = W_1,$$

say. Let V be a closed neighbourhood of $\overline{S}$ contained in W_1, and put $N = \overline{X} \setminus V$.

We show that $M = \gamma^+(\overline{N})$ is the required absorbing set. We prove first that, given $u \in V \setminus \overline{S}$, there is a $t > 0$ such that $ut \in N$. For if this assertion is false, we could define inductively $t_i \in G$ by requiring that $u1 \in U(h^*, t_0)$ and $u(1 + t_0 + \ldots + t_{i-1}) \in U(h^*, t_i)$. Then, from (3.2),

$$\alpha(t_0 + \ldots + t_n, u1) \geq (1 + h^*)^{n+1}. \tag{3.3}$$

Now, by Lemma 3.1(iii), $u1 \in \overline{X} \setminus \overline{S} \cap X \subset X \setminus S$. Therefore, from (3.3), for each n,

$$P\left(u(1 + t_0 + \ldots + t_n)\right) \geq (1 + h^*)^{n+1} P(u1),$$

which contradicts the boundedness of P.

We finally prove that M is compact. From what has just been proven, given any $u \in \overline{N}$, there is a $t_u > 0$ such that $ut_u \in N$. By continuity, for each such u, there is an open neighbourhood $V(u)$ of u in $\overline{N}$ such that $V(u)t_u \in \overline{N}$. By compactness, we may choose u_i such that $\bigcup_{i=1}^{i=n} V(u_i) = \overline{N}$, and clearly

$$M = \bigcup_{i=1}^{i=n} \overline{V(u_i)}[0, t_{u_i}]$$

is compact.

Now M is forward invariant, therefore $\gamma^+(\overline{N}) \subset M$ and so $\gamma^+(\overline{N}) = M$. Since $\overline{X} \setminus \overline{S}$ is open and forward invariant(by Lemma 3.1(iii)), it follows that $d(M, \overline{S}) > 0$. As every semi-orbit intersects N, the proof is complete.

4. Permanent coexistence for the reaction-diffusion system. Theorem 3.2 is now applied to the system of partial differential equations (1.1) to obtain a criterion for permanent coexistence. Let $\phi : Y \cap \mathring{\mathbf{R}}_+^n \to \mathbf{R}^+$ be a strictly positive bounded C^1 function. Noting that, by Lemma 3.1(i), if $u \subset X \setminus S$ each of its components is strictly positive, we define

$$P(u) = \exp\left(\int_{\overline{D}} \log \phi\,(u(x))\; dx\right) \quad (u \in X \setminus S).$$

With 'dot' denoting differentiation along an orbit, from the partial differential equations (1.1a) and use of the divergence theorem, for $u \in X \setminus S$,

$$\begin{aligned} \alpha(t,u) &= P(ut)/P(u) \\ &= \exp\left(\int_{\overline{D}} \log\left(\phi\left(u(x,t)\right)/\phi\left(u(x,0)\right)\right)\, dx\right) \\ &= \exp\left(\int_0^t ds \int_{\overline{D}} \dot{\phi}\,\left(u(x,s)\right)/\phi(u(x,s))dx\right) \\ &= \exp\left(\int_0^t ds \int_{\overline{D}} \left(\psi\left(u(x,s)\right) + Q\left(u(x,s)\right)\right)\, dx\right), \end{aligned} \tag{4.1}$$

where

$$\psi(u) = \phi^{-1} \sum_{i=1}^{i=n} \frac{\partial \phi}{\partial u_i} u_i f_i(u), \tag{4.2}$$

$$(4.3)\qquad Q(u) = -\sum_{i=1}^{i=n}\sum_{j=1}^{j=m} \mu_i \frac{\partial}{\partial x_j}\left(\phi^{-1}\frac{\partial \phi}{\partial u_i}\right)\frac{\partial u_i}{\partial x_j}.$$

The function $\psi : Y \cap \mathring{\mathrm{R}}^n_+ \to \mathbf{R}$ is clearly continuous, and its (lower semi-continuous) extension to Y, also denoted by ψ, is defined by

$$\psi(u) = \liminf_{\substack{v\to u\\ v\in X\setminus S}} \psi(v).$$

THEOREM 4.1. *Assume that* (H1) *and* (H2) *hold. Let* $\phi : Y \cap \mathring{R}^n_+ \to \mathbf{R}^+$ *be a strictly positive bounded* C^1 *function. With* ψ *and* Q *defined by* (4.2) and (4.3) *respectively, assume that*

(i) ψ *is bounded below on* $Y \cap \mathbf{R}^n_+$, *and for some* $\tau > 0$,

$$(4.4)\qquad \sup_{t\ge\tau}\int_0^t ds \int_{\overline{D}} \psi\left(u(x,s)\right)dx > 0 \quad \left(u \in \overline{\Omega(\overline{S})}\right);$$

(ii) $Q(u) \ge 0 \quad (u \in X \setminus S)$.

Then the system (1.1) is permanently coexistent.

PROOF. Evidently $P : X\setminus S \to \mathbf{R}_+$ is continuous, bounded above, and strictly positive. With

$$\Phi(t,u) = \exp\left(\int_0^t ds\int_{\overline{D}}\psi\left(u(x,s)\right)ds\right),$$

from (4.1) and condition (ii) above, $\alpha(t,u) \ge \Phi(t,u)$ for $u \in X \setminus S$. Since ψ is bounded below, (3.1b) obviously holds. Also, since

$$(4.5)\qquad \liminf_{\substack{v\to u\\ v\in X\setminus S}} \psi\left(v(x,t)\right) \ge \liminf_{\substack{w\to u(x,t)\\ w\in Y\cap\mathring{\mathrm{R}}^n_+}} \psi(w) = \psi\left(u(x,t)\right),$$

from Fatou's lemma (after adding a constant if necessary to make the integrand non-negative),

$$(4.6)\qquad \liminf_{\substack{v\to u\\ v\in X\setminus S}} \int_0^t ds\int_{\overline{D}}\psi\left(v(x,s)\right)dx \ge \int_0^t ds\int_{\overline{D}}\psi\left(u(x,s)\right)dx.$$

Therefore, for $u \in \overline{\Omega(\overline{S})}$,

$$\begin{aligned}\sup_{t\geq\tau}\alpha(t,u) &= \sup_{t\geq\tau}\liminf_{\substack{v\to u\\ v\in X\setminus S}}\alpha(t,v) \geq \sup_{t\geq\tau}\liminf_{\substack{v\to u\\ v\in X\setminus S}}\Phi(t,v)\\ &\geq \sup\exp\left(\int_0^t ds\int_{\overline{D}}\psi\left(u(x,s)\right)dx\right) \quad \text{(from (4.6))},\\ &> 1 \quad \text{(from (4.4))}.\end{aligned}$$

This verifies condition (3.1a), and the existence of a compact absorbing set at non-zero distance in the sup norm from $\overline{S}$ follows, since by (H2) all orbits eventually reach $\overline{X}$. An application of Lemma 2.2 yields the corresponding L^1 lower bound, and this completes the proof.

Concerning the conditions of the theorem, an inequality of the form (ii) is necessary in Liapunov functional methods for reaction-diffusion systems, see for example [**1**]. The condition ensuring that orbits are uniformly repelled by $\overline{S}$ is (4.4), a much weakened version of the usual requirement for a Liapunov functional.

5. An application. When applying Theorem 4.1, knowledge of the Ω-limit set of the boundary is clearly crucial, that is, the asymptotic behaviour of the $(n-1)$ species subsystems obtained by setting one component zero must be known. For a pair of reaction-diffusion equations, a fair amount of information of this type is available, and it turns out that under Neumann boundary conditions the Ω-limit sets are often equilibria of the kinetic equations. For three equations without diffusion the asymptotic behaviour may be extremely complex even for simple reaction terms, and the presence of diffusion will of course further complicate matters. However, so far as permanent coexistence is concerned, three species systems are relatively tractable. The following simple consequence of Theorem 4.1 will enable us to show that indeed, in such a context, the permanent coexistence of the corresponding kinetic system (which has been studied in a variety of cases, see [**9**] for example) is often enough to ensure that of the reaction-diffusion system.

LEMMA 5.1. *Assume that* (H1) *and* (H2) *hold. Suppose also that* $\Omega(\overline{S})$ *consists of a finite number of spatially homogeneous equilibria* $\overline{u}_1,\ldots,\overline{u}_k$, *say. Then the system* (1.1) *is permanently coexistent if* *there exist* $\alpha_1, \ldots, \alpha_n > 0$ *such that*

$$\sum_{i=1}^{i=n} \alpha_i f_i(\overline{u}_j) > 0 \quad (j = 1, \ldots, k).$$

PROOF. With $\phi(u) = \prod_{i=1}^{i=n} u_i^{\alpha_i}$,

$$\phi(\overline{u}_j) = \sum_{i=1}^{i=n} \alpha_i f_i(\overline{u}_j) > 0$$

and

$$Q(u) = \sum_{i=1}^{i=n} \sum_{j=1}^{j=m} \mu_i \alpha_i \left(u_i^{-1} \frac{\partial u_i}{\partial x_j} \right)^2 \geq 0,$$

so the conditions of Thoerem 4.1 are verified.

As an application we study a three species system modelling the interaction of two prey and a predator, the reaction terms being of Lotka-Volterra type. With u_1, u_2, the densities of the prey, and u_3 that of the predator, consider the system

$$\begin{aligned}
\frac{\partial u_1}{\partial t} &= u_1(a_1 - \varepsilon_{11}u_1 - \varepsilon_{12}u_2 - \alpha_1 u_3) + \mu_1 \Delta u_1 \\
\frac{\partial u_2}{\partial t} &= u_2(a_2 - \varepsilon_{11}u_1 - \varepsilon_{22}u_2 - \alpha_2 u_3) + \mu_2 \Delta u_2 \\
\frac{\partial u_3}{\partial t} &= u_3(-c + \beta_1 u_2 + \beta_2 u_2 - \gamma u_3) + \mu_3 \Delta u_3,
\end{aligned}$$

with homogeneous Neumann conditions on ∂D, the $a_i, \varepsilon_{ij}, \alpha_i, \beta_i, c, r$ and μ_i being strictly positive constants. Let

$$B = \begin{bmatrix} \varepsilon_{11} & \varepsilon_{12} & \alpha_1 \\ \varepsilon_{21} & \varepsilon_{22} & \alpha_2 \\ -\beta_1 & -\beta_2 & \gamma \end{bmatrix}.$$

THEOREM 5.2. *Let* D *be as in* (H1). *Then the above system is permanently coexistent whenever the corresponding kinetic system has this property. This is the case if all of the following are satisfied:*

(a) $\det B > 0$;

(b) *at least one of* $a_1\varepsilon_{22} > a_2\varepsilon_{12}, a_2\varepsilon_{11} > a_1\varepsilon_{21}$ *holds; and*

(c) *there is an equilibrium of the kinetic system in* $\mathbf{R}^n_+$. vskip7pt

PROOF. The two species subsystems obtained by putting u_1, u_2, and u_3 zero in $\overline{D}$ in turn must first be examined. If $u_3 = 0$, a competing species system is obtained, and it follows from [**3**] that the Ω-limit sets are constant equilibria. The same conclusion follows from [**12**] in the predator-prey systems obtained by setting u_1 or u_2 zero. The conditions of Lemma 5.1 are thus satisfied, and the rest is elementary algebra, the result following from [**10**].

As is shown in [**10**], conditions (a), (b), and (c) are essentially necessary, for if (c) does not hold, the system is not permanently coexistent, whilst if $\det B < 0$ or both the inequalities in (b) are reversed the same conclusion follows. For the kinetic system, and so for the reaction-diffusion system, there can be a limit cycle and yet permanent coexistence can hold. For the reaction-diffusion system, more complex behaviour is possible, and in particular it is known that a stable stationary spatially inhomogeneous solution (a pattern) can exist, see [**11**]. The above analysis is also applicable for more general reaction terms. for example when there is a switching predator, the only difference being that the conditions for the kinetics system are more complex, see [**7**].

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