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Contributions of Alan C. Lazer to mathematical population dynamics *

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Abstract

This paper is a survey of the contributions that Professor Alan C. Lazer has made to the mathematical theory of population dynamics. Specific areas where Professor Lazer has made important contributions include time periodic population models with diffusion and nonautonomous models for many competing species.

1 Introduction

This article will describe some of the contributions that Alan Lazer has made to mathematical population dynamics. Those contributions include:

- General and abstract results on competitive systems and on periodic-parabolic problems
- Results and methods for nonautonomous systems of ordinary differential equations, specifically in the context of competition models
- Various specific results on stability, the existence of traveling wavefronts, and other problems in the theory of reaction-diffusion models. Professor Lazer's papers contributing to the development of population dynamics include [3-10,14,15,20,23-26].

In addition to his direct mathematical contributions, Professor Lazer has personally influenced, inspired, and/or collaborated with many other mathematicians working in the area. Those include, among others, S. Ahmad, C. Alvarez, R.S. Cantrell, A. Castro, E.N. Dancer, P. Hess, A. Leung, P.J. McKenna, F. Montes de Oca, D. Murio, D. Sanchez, and the author of this survey. The remainder of the survey is divided into three sections: a section covering the period from the early 1980's to the early 1990's, with a focus on models for two competing species with diffusion and/or periodic time dependence; a section covering the period from the early 1990's to the present, with a focus on models for many

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competitors with arbitrary time dependence; and a brief concluding section. Some references are made to papers that use or build upon Professor Lazer's ideas, but those are simply examples; there has been no attempt to make a comprehensive listing of such work.

2 Eigenvalues, Periodicity, and Pairs of Competing Species

One of the most basic models in population dynamics is the logistic equation

$$\frac{du}{dt} = (a - bu)u \tag{2.1}$$

where u represents a population density (so that only solutions with $u \geq 0$ are physically meaningful), a represents the population growth rate at low densities, and $b > 0$ represents the self-regulatory effects of crowding on the population. The logistic equation always has the nonnegative equilibrium $u = 0$, and if $a > 0$ it also has the positive-equilibrium a/b. If $a > 0$ and $u(0) > 0$ then $u \to a/b$ as $t \to \infty$. If $a \leq 0$ and $u(0) \geq 0$ then $u \to 0$ as $t \to \infty$. Linearizing (2.1) around $u = 0$ gives $dy/dt = ay$, so $u = 0$ is locally stable if $a \leq 0$, asymptotically in the case $a < 0$, and unstable if $a > 0$; similarly linearizing around a/b when $a > 0$ yields $dz/dt = -az$, so in that case $u = a/b$ is locally stable. It is clear from the above discussion that the sign of a is crucial in determining the behavior of (2.1). The general ideas of stability, instability, and bifurcation apply to models much more general than (2.1) but in cases with time dependent coefficients, or diffusion, or both, we need a criterion that can replace checking the sign of a. The extension of the logistic equation (2.1) and other models to cases with periodicity and diffusion is important from the applied viewpoint because many ecological systems are affected by seasonal changes and most populations are dispersed in space.

Periodic Systems of Ordinary Differential Equations: Floquet Theory

If $A(t)$ is an $n \times n$ matrix with continuous T-periodic coefficients, it follows from the results of Floquet theory that the system

$$\frac{d\vec{y}}{dt} = A(t)\vec{y} \tag{2.2}$$

has a fundamental matrix $\Phi(t)$ of the form $\Phi(t) = P(t)\exp(tR)$ where $P(t)$ is T-periodic. (If A is a constant then we may take $\mathbf{P} = I$ and $R = A$.) The characteristic exponents of the system are the eigenvalues $\{\rho_i\}$ of R. (The Floquet multipliers are $\{e^{T\rho_i}\}$.) If $\operatorname{Re}\rho_i < 0$ for $i = 1, \ldots, n$ then the solution $\vec{y}(t) \equiv 0$ is stable, so the characteristic exponent with the largest real part plays a role analogous to a in (2.1).

Elliptic Eigenvalues and Diffusion

The parabolic equation

$$\begin{aligned} u_t &= d\Delta u + ru \quad \text{in} \quad \Omega \\ \alpha\frac{\partial u}{\partial \vec{n}} + \beta u &= 0 \quad \text{on} \quad \partial\Omega\,, \end{aligned} \tag{2.3}$$

where $\Omega \subseteq \mathbb{R}$ is a bounded domain and where $\alpha, \beta \geq 0,\ \alpha + \beta > 0$, can be solved via separation of variables to obtain $u = \sum_{n=1}^{\infty} c_n e^{\rho_n t}\phi_n(x)$ where ρ_n and $\phi_n(x)$ are the nth eigenvalue and eigenfunction respectively for the problem

$$\begin{aligned} d\Delta\phi + r\phi &= \rho\phi \quad \text{in} \quad \Omega \\ \alpha\frac{\partial \phi}{\partial \vec{n}} + \beta\phi &= 0 \quad \text{on} \quad \partial\Omega\,. \end{aligned} \tag{2.4}$$

The classical variational theory of (2.4) implies that the eigenvalues $\{\rho_i\}$ are real, with $\rho_1 > \rho_2 \geq \rho_3 \ldots$. If $\rho_1 < 0$ then all solutions to (2.3) will approach zero as $t \to \infty$; if $\rho_1 > 0$ at least some will grow. Furthermore, the eigenfunction $\phi_1(x)$ corresponding to ρ_1 is positive in Ω and ρ_1 is a simple eigenvalue. For these reasons ρ_1 is called the principal eigenvalue for (2.4). More general elliptic operators may fail to be self-adjoint and thus may admit complex eigenvalues. However, since second order elliptic operators satisfy the maximum principle, and typically have compact resolvents on appropriate function spaces, the Krein-Rutman theorem may be used to show that the eigenvalue problem

$$\begin{aligned} \sum_{i,j=1}^{m} a_{ij}(x)\phi_{x_i x_j} + \sum_{i=1}^{n} b_i(x)\phi_{x_i} + c(x)\phi = \rho\phi \quad \text{in} \quad \Omega \\ \alpha(x)\frac{\partial \phi}{\partial \vec{n}} + \beta(x)\phi = 0 \quad \text{on} \quad \partial\Omega \end{aligned} \tag{2.5}$$

has a principal eigenvalue ρ_1 with positive eigenfunction ϕ_1. (This assumes the coefficients of (2.5) and the boundary of Ω are reasonably smooth.) It turns out that $\rho_1 > \operatorname{Re}\rho_n$ for $n > 1$, but that requires additional arguments beyond the Krein-Rutman theorem. See [11,32] for details.

Principal Eigenvalues of Periodic-Parabolic Operators

We now can describe one of Alan Lazer's contributions to population dynamics. Suppose that $\Omega \subseteq \mathbb{R}^n$ is bounded with smooth boundary. Let

$$Lu = u_t - \sum_{i,j=1}^{n} a_{ij}(x,t)u_{x_i x_j} - \sum_{i=1}^{n} b_i(x,t)u_{x_i} - c(x,t)u, \tag{2.6}$$

and assume that the coefficients are Hölder continuous and T-periodic, and that $((a_{ij}))$ is symmetric and uniformly positive definite. Suppose that $\alpha(x)$ and $\beta(x)$ are nonnegative Hölder continuous functions on $\partial\Omega$ with $\alpha + \beta > 0$.

Theorem 2.1 (Lazer, Castro and Lazer [14,23]) *There exist a real number σ_1 and a T-periodic function $\phi_1(x,t) \in C^{2+\alpha,1+\alpha/2}(\overline{\Omega} \times \mathbb{R})$ which is positive on $\Omega \times \mathbb{R}$ such that*

$$\begin{aligned} L\phi = \sigma_1 \phi \quad &in \quad \Omega \times \mathbb{R} \\ \alpha(x)\frac{\partial \phi}{\partial \vec{n}} + \beta(x)\phi = 0 \quad &on \quad \partial\Omega\,. \end{aligned} \tag{2.7}$$

Remarks: Note that if L and ϕ_1 were independent of t then we would have $\sigma_1 = -\rho_1$ where ρ_1 is the principal eigenvalue in (2.5). The proof of this theorem is based on the Krein-Rutman Theorem, as in the nonselfadjoint elliptic case. A key step involves showing that $(L+K)^{-1}$ exists if K is a large positive constant; this is accomplished via a result of Kolesov on the existence of periodic solutions between sub- and super-solutions [22].

Once σ_1 is available it is possible to use ϕ_1 to construct sub- and/or super-solutions to nonlinear problems, apply bifurcation theory, degree theory, etc., and generally extend much of the theory of nonlinear elliptic eigenvalue problems. Periodic-parabolic logistic equations and Lokta-Volterra models are discussed in detail by Hess in [19]. A typical result is:

Theorem 2.2 ([19]) *The T-periodic parabolic logistic equation*

$$\begin{aligned} u_t - \sum_{i,j=1}^{n} a_{ij}(x,t)u_{x_i,x_j} - \sum_{i=1}^{n} b_i(x,t)u_{x_i} = (c(x,t) - m(x,t)u)u \quad &in\ \Omega \times (0,\infty) \\ \alpha(x)\frac{\partial u}{\partial \vec{n}} + \beta(x)u = 0 \quad on \quad \partial\Omega \times (0,\infty)& \end{aligned} \tag{2.8}$$

has a unique postive T-periodic solution $u^*(x,t)$ if and only if $\sigma_1 < 0$ in (2.7), where L is the operator in (2.6). (The coefficients in (2.8) are the same as in (2.6).) If $\sigma_1 < 0$ then u^* is globally attracting among positive solutions. If $\sigma_1 \geq 0$ then all nonnegative solutions of (2.8) approach zero as $t \to \infty$.

Remarks: It is clear from Theorem 2.2 that $-\sigma_1$ plays the same role in (2.8) that a plays in (2.1). By combining the use of the principal eigenvalue of (2.7) with other ideas introduced by Professor Lazer it is possible to give a comprehensive treatment of Lotka-Volterra models with diffusion and time periodicity; see for example [19]. We now turn to some of those other ideas.

Periodic and Diffusive Lotka-Volterra Models

Just as the logistic equation is the simplest model for a single population which accounts for the effects of crowding, Lotka-Volterra models are the simplest models of density-dependent interactions between species. If u_i denotes the population density of the ith species, the basic Lotka-Volterra competition model is

$$\frac{du_i}{dt} = (a_i - b_{ii}u_i - b_{ij}u_j)u_i, \;\; i = 1, 2, \;\; j \neq i. \tag{2.9}$$

It is easy to see via phase plane analysis that if

$$a_i > a_j b_{ij}/b_{jj} \quad \text{for} \quad i = 1,2,\ j \neq i, \tag{2.10}$$

then there is a unique equilibrium (u_1^*, u_2^*) with both components positive which is globally attracting among solutions that have both components positive initially. If (2.10) fails then generally the model either predicts that one of the competitors always becomes extinct while the other persists, or that the outcome of the competition depends on the initial data. Another feature of the system (2.9) is that if (u_1, u_2) is a solution which is nonnegative in both components then the change of variables $(v_1, v_2) = (u_1, -u_2)$ converts (2.9) to a cooperative system. Cooperative systems are well known to be order preserving so if (u_1, u_2) and $(\tilde{u}_1, \tilde{u}_2)$ are nonnegative solutions to (2.9) with $u_1(0) \geq \tilde{u}_1(0)$ and $u_2(0) \leq \tilde{u}_2(0)$ then $u_1(t) \geq \tilde{u}_1(t)$ and $u_2(t) \leq \tilde{u}_2(t)$ for all $t > 0$. (See for example [15,19,27,37] for more details.) This order preserving property extends via the maximum principle to the Lotka-Volterra model with diffusion

$$\begin{aligned} u_{i_t} &= d_i \Delta u_i + [a_i - b_{ii} u_i - b_{ij} u_j] u_i \quad \text{in} \quad \Omega \times (0, \infty), \\ \alpha_i \frac{\partial u_i}{\partial \vec{n}} &+ \beta_i u_i = 0 \quad \text{on} \quad \partial\Omega, \quad \text{for} \quad i = 1,2,\ \ j \neq i\,. \end{aligned} \tag{2.11}$$

In the case of Neumann conditions in (2.11), solutions to (2.9) will also be solutions to (2.12). If (2.10) holds, then positive solutions to (2.9) approach (u_1^*, u_2^*) as $t \to \infty$. If $(u_1(x,t), u_2(x,t))$ is a positive solution of (2.11) under Neumann boundary conditions, then by choosing solutions $(\overline{u}_1(t), \underline{u}_2(t))$ and $(\underline{u}_1(t), \overline{u}_2(t))$ of (2.9) such that $\underline{u}_i(0) \leq u_i(x,0) \leq \overline{u}_i(0)$ for $i = 1,2$ we can see that $(u_1, u_2) \to (u_1^*, u_2^*)$ as $t \to \infty$ since $\overline{u}_i(t) \geq u_i(x,t) \geq \underline{u}_i(t)$ and $\overline{u}_i$, $\underline{u}_i \to u_i^*$ as $t \to \infty$. This is essentially the method of contracting rectangles (see [37].) However, in cases where (2.11) has boundary conditions other than Neumann, or where the coefficients of (2.9) or (2.11) are allowed to depend on t, this approach fails. By using methods based on sub- and super-solutions, Leung [28,29] and Pao [31] showed that the model (2.11) with Dirichlet boundary conditions the system (2.11) has a positive equilibrium if

$$a_i > d_i \lambda_1 + a_j b_{ij}/b_{jj}, \ \ i = 1,2, \ \ j \neq i. \tag{2.12}$$

At around the same time, Gopalsamy [17,18] showed that the system (2.9) with $a_i = a_i(t)$ T-periodic has a positive stable T-periodic steady-state provided

$$\min(a_i) > b_{ij} \max(a_j)/b_{jj}, \ \ i = 1,2,\ j \neq i\,. \tag{2.13}$$

In [14], Professor Lazer and I obtained some stability criteria for equilibria of (2.11) and showed that if $a_1 = a_2 = a$ in (2.11) then the condition (2.12) can be replaced by the conditions $a > d_i \lambda_1,\ i = 1,2$, and $b_{jj} > b_{ij},\ i = 1,2,\ j \neq i$. The most important idea in that paper, however, was an extension of Gopalsamy's result to the case of (2.11) with Neumann boundary conditions. Specifically, we showed that for (2.11) with Neumann boundary conditions and $a_i = a_i(t)$ periodic in time that under condition (2.13) the solution to (2.9) obtained by

Gopalsamy is also stable for (2.11). A key observation was that although the periodicity of the system made a simple argument based on contracting rectangles impossible, it was still possible to construct solutions $(\overline{u}_1, \underline{u}_2)$, $(\underline{u}_1, \overline{u}_2)$ depending only on t and having the property $\overline{u}_i(t+T) \leq \overline{u}_i(t)$, $\underline{u}_i(t+T) \geq \underline{u}_i(t)$, even though $\overline{u}_i(t)$, $\underline{u}_i(t)$ were not in general monotone in t. Another way to express the idea would be that although the original system does not admit contracting rectangles, the period map (i.e. Poincaré map) of the system does. I thought that we had just found an interesting variant on results that were already known in the autonomous case, but Professor Lazer had the deeper insight that the methods used in [15] were a special case of something much more general and abstract.

In the work with C. Alvarez [10], Professor Lazer showed that in the case of (2.9) where all of the coefficients are T-periodic, the system has an attracting periodic steady state which is globally attracting among positive solutions provided

$$\min(a_i) > \max(a_j) \max(b_{ij}) / \min(b_{ii}) \quad i = 1, 2, \ \ j \neq i\,. \tag{2.14}$$

Again, the key idea was to look at the Poincaré map. In this context Alvarez and Lazer used Floquet theory (and various estimates) to show that *any* periodic solution is locally stable. That observation made it possible to compute the topological degree at any fixed point of the period map, so that existence and uniqueness results could be obtained via degree theory.

Continuing the development

Continuing to develop the ideas introduced in [10,15], Professor Lazer and S. Ahmad showed in [3] that for the diffusive system (2.11) with Neumann boundary conditions and with a_i, b_{ij}, and b_{jj} periodic in time (and possibly varying in space) the condition (2.14) implies the existence of a coexistence state, while if (2.14) holds for (say) $i = 1$ and is reversed for $i = 2$ then $u_2 \to 0$ as $t \to \infty$. Again, the key idea was to use something analogous to contracting rectangles, but for the Poincaré map.

Abstract Competition Systems and their Implications

A key idea in the papers [10,14,23] was to look at a periodic system from the viewpoint of the Poincaré map. Using the order preserving properties of models for two competing species then permits the construction, in some cases, of something analogous to contracting rectangles for the Poincaré map. In [20], Professor Lazer and Peter Hess gave an abstract formulation of this idea in the context of a discrete dynamical system acting on an ordered Banach space with an ordering of the sort which is typically preserved by models for two competitors. (An ordered Banach space is simply a Banach space E with an ordering defined by a positive cone P, which is just a subset of E with the properties that if $x, y \in P$ and $c \in \mathbb{R}$, $c > 0$ then $x + y \in P$ and $cx \in P$. In that setting we write $x \geq y$ if $x - y \in P$. For a detailed discussion see [11].)

We shall first describe the set-up of [20], make a few key definitions, and then state the main result of [20] and describe its implications. Let E_1 and E_2 be ordered Banach spaces whose orderings are defined by the positive cones P_1 and P_2 respectively. Assume that the interiors of P_1 and P_2 are nonempty. Define an ordering on $E_1 \times E_2$ by $(x_1, x_2) \leq (y_1, y_2) \Leftrightarrow x_1 \leq y_1,\ x_2 \geq y_2$. (This is the type of ordering which is typically preserved by models of two competitors.) Suppose that $F : E_1 \times E_2 \to E_1 \times E_2$ is smooth and order preserving. Iterating F then leads to a semidynamical system which is a suitable abstraction of the Poincaré map. Recall that if E is an ordered Banach space and $a, b \in E$ with $a \leq b$ then the *order interval* $[a, b]$ is the set $\{x \in E : a \leq x \leq b\}$. Also, recall that $x > y$ means $x \geq y,\ x \neq y$ and that $x >> y$ means $x - y$ is in the interior of the positive cone. Suppose that $F(x_1, x_2) = (f_1(x_1, x_2), f_2(x_1, x_2))$. Assume that F satisfies the following hypotheses:

(A1) F maps bounded positive order intervals into compact sets, i.e. F is order compact.

(A2) $f_1(0, x_2) = 0$ and $f_2(x_1, 0) = 0$ for all $x_1 \in E_1,\ x_2 \in E_2$

(A3) $0 << f_1(x_1, x_2) << f_1(x_1', x_2'), \quad 0 << f_2(x_1', x_2') << f_2(x_1, x_2)$ if $0 < x_1 \leq x_1',\ \ 0 < x_2' \leq x_2,\ \ (x_1, x_2) \neq (x_1', x_2')$.

(A4) there exist unique fixed points $\hat{x}_1 = f_1(\hat{x}_1, 0),\ \ \hat{x}_2 = f_2(0, \hat{x}_2)$, such that $\tau\hat{x}_1 << f_1(\tau\hat{x}_1, 0) << \hat{x}_1$ for $0 < \tau < 1,\ \ \hat{x}_1 << f_1(\tau\hat{x}_1, 0) << \tau\hat{x}_1$ for $\tau > 1$, and similarly for $\hat{x}_2, f_2$

(A5) the derivatives $D_1 f_1$ and $D_2 f_2$ satisfy

$$D_1 f_1(0, \hat{x}_2) : P_1 - \{0\} \to \text{Int} \quad P_1$$
$$D_2 f_2(\hat{x}_1, 0) : P_2 - \{0\} \to \text{Int} \quad P_2$$

Remarks: Hypotheses (A1) and (A5) are needed for various technical reasons; hypotheses (A2)-(A4) capture essential features of competition models. If x_1, x_2 are viewed as population densities, (A2) says that if one of the populations is initially zero it will remain zero; (A3) says that increasing the density of either population reduces the growth rate of both, and (A4) says that each species has a stable positive equilibrium density when the other is absent.

Assumptions (A1) and (A5) together with the Krein-Rutman theorem imply that the maps $D_1 f_1(0, \hat{x}_2)$ and $D_2 f_2(\hat{x}_1, 0)$ have positive principal eigenvalues λ_1 and λ_2.

Definition: (Lazer and Hess [20]). The mapping F is *compressive* if it has an order interval in $\text{Int}P_1 \times \text{Int}P_2$ which is globally attracting in $(P_1 - \{0\}) \times (P_2 - \{0\})$.

Remarks: If F has a globally attracting fixed point which is positive in both components then F is compressive. More generally, if F is compressive then eventually the densities of both competitors will be bounded away from zero so the competitors will coexist. A related notion is permanence or uniform persistence, but that notion does not involve any order preserving properties. For a discussion of these and other notions of persistence see [16].

We can now state the main abstract result of [20].

Theorem 2.3 (Lazer and Hess [20]) *The mapping F is compressive if the principal eigenvalues λ_1 and λ_2 of*

$$\begin{aligned} D_1 f_1(0, \hat{x}_2) v_1 &= \lambda_1 v_1 \\ D_2 f_2(\hat{x}_1, 0) v_2 &= \lambda_2 v_2 \end{aligned} \tag{2.15}$$

are both larger than 1, i.e. $\lambda_1, \lambda_2 > 1$.

Discussion: The mapping F could be taken to be the Poincaré map of a periodic competition model with diffusion. The order preserving properties would then follow from those for parabolic competition systems, whose order preserving properties follow from arguments based on the maximum principle. Parabolic regularity results imply the compactness of F on various function spaces. In the context where F is the Poincaré map for periodic-parabolic competition system, the linearized operators $D_1 f_1(0, \hat{x}_2)$ and $D_2 f_2(\hat{x}_1, 0)$ will be the Poincaré maps for two single linear periodic-parabolic operators. If L is a periodic-parabolic operator of the form (2.6) and σ_1 is the principal eigenvalue in (2.7) then the Poincaré map defined by $Mu(x) = v(x, T)$ where v satisfies $Lv = 0$ in $\Omega \times (0, T)$, $\alpha \partial v / \partial \vec{n} + \beta v = 0$ on $\partial\Omega \times (0, T)$, $v(x, 0) = u(x)$ has the principal eigenvalue $\lambda = e^{-\sigma_1 T}$. Thus, λ is in a sense analogous to a Floquet multiplier while $-\sigma_1$ is analogous to a characteristic exponent.

The key hypothesis of Theorem 2.3 is that the principal eigenvalues λ_1, λ_2 of (2.15) are both larger than 1. The eigenvalue problem $D_1 f_1(0, \hat{x}_2) v_1 = \lambda_1 v_1$ corresponds to the linearization of f_1 around the equilibrium $(0, \hat{x}_2)$. The condition $\lambda_1 > 1$ implies that a population satisfying $x_1(t+1) = Df_1(0, \hat{x}_2) x_1(t)$ would grow exponentially. The condition $\lambda_2 > 1$ has an analogous interpretation. Together, they essentially mean that the density of either species will increase if that species is introduced at a low density when the other species is already established. Thus, Theorem 2.3 is a rigorous version of the notion that mutual invasibility implies coexistence.

As a concrete application of Theorem 2.3, consider the system

$$\begin{aligned} &L_i u_i = [a_i(x,t) - b_{ij}(x,t) u_i - b_{ij}(x,t) u_j] u_i \quad \text{in} \quad \Omega \times (0, \infty) \\ &\alpha_i(x) \frac{\partial u_i}{\partial \vec{n}} + \beta_i(x) u_i = 0 \quad \text{on} \quad \partial\Omega \times (0,\infty), \;\; i = 1, 2, \;\; j \neq i\,. \end{aligned} \tag{2.16}$$

where L_i is as in (2.6) and the coefficients a_i, b_{ii}, b_{ij} are Hölder continuous in both variables and T-periodic in t. Suppose that the principal eigenvalues of the problems

$$\begin{aligned} (L_i - a_i)\psi = \sigma\psi \quad &\text{in} \quad \Omega \times (0, \infty), \\ \alpha_i \frac{\partial \psi}{\partial \vec{n}} + \beta_i \psi = 0 \quad &\text{on} \quad \partial\Omega \times (0, \infty), \\ \psi \quad T-&\text{periodic} \end{aligned}$$

for $i = 1, 2$ are both negative so that the logistic equations obtained by setting $u_j = 0$ in (2.16) both have single species steady-state solutions by Theorem 2.2. Denote those solutions by u_i^*, $i = 1, 2$; then $(u_1^*, 0)$ and $(0, u_2^*)$ are steady-state solutions for (2.16). To apply Theorem 2.3 we would use, for example, $\hat{x}_1 = (u_1^*(x,0), 0), \hat{x}_2 = (0, \hat{u}_2^*(x,0))$ and take F to be the Poincaré map for (2.16). It is reasonably straightforward to verify that Theorem 2.3 applies in this situation; see the discussion in [19] or [20]. By theorem 2.3, the system (2.16) is compressive if the principal eigenvalues of

$$
\begin{aligned}
&(L_i - a_i + b_{ij} u_j^*)\psi = \sigma\psi \quad \text{in} \quad \Omega \times (0, \infty) \\
&\alpha_i \frac{\partial \psi}{\partial \vec{n}} + \beta_i \psi = 0 \quad \text{on} \quad \partial\Omega \times (0, \infty) \\
&\psi \quad T - \text{periodic}
\end{aligned}
\tag{2.17}
$$

are both negative for $i = 1, 2, \quad j \neq i$. (This result can be set in $[C^{2+\alpha}(\overline{\Omega})]^2$ or $[W^{2,p}(\Omega)]^2$, among other possible function spaces.) The condition that the principal eigenvalues be negative in (2.17) for $i = 1, 2$ generalizes most of the previous conditions for the existence of a steady-state of (2.16) which is positive in both components. For example, systems with constant coefficients are periodic with every period T, and for such systems the condition (2.12) implies the negativity of the eigenvalues in (2.17) via simple estimates of the eigenvalues. However, condition (2.12) is less sharp than the requirement of negativity of the eigenvalues in (2.17). Various other previous results, including those of [3], can be recovered, improved, or unified by applications of Theorem 2.3; see [19,20] for detailed discussions.

Related Ideas and Applications of Periodic-Parabolic Eigenvalues

Theorem 2.3 gives a good criterion for coexistence in competition models, but there are other problems in population dynamics and other analytic approaches where the existence of principal eigenvalues for periodic-parabolic operators plays a crucial role. Many techniques of nonlinear analysis, such as degree theory and bifurcation theory, depend on a knowledge of the eigenvalues of linearized operators. Constructions of sub- and supersolutions often involve eigenfunctions. Some of these ideas are discussed in [13,19]. For systems such as predator-prey models which do not have simple order-preserving properties, the notion of compressivity must often be replaced with that of permanence, i.e. uniform persistence plus dissipativity. A semidynamical system on an ordered Banach space is permanent if there is a bounded subset of the interior of the positive cone which is also uniformly bounded away from the boundary of the positive cone and which is globally attracting positive trajectories of the system. (See [21] for a discussion.) A key point in establishing permanence is to show that steady-states with one or more species absent are unstable in the sense that if they are perturbed by adding one of the missing species at low densities then the population of density of that introduced species will increase. To apply the idea of permanence to a periodic-parabolic model, the first step is to convert the time-dependent problem into a semidynamical system by writing it as a skew-product flow (see [35]) and establish that it is dissipative; the second step is to analyze the stability of steady-states; and the final step is to apply an appropriate abstract result to conclude that the system is indeed permanent. Eigenvalues and eigenfunctions are used in the stability analysis; see for example [12]. (A comparison of the ideas of compressivity, permanence, and practical persistence is given in [16].)

3 Systems with Many Competitors

Persistence and Convergence in Nonautonomous Systems: Uniform Conditions

If the competition model (2.9) is extended to include N competing species, the resulting system is

$$\frac{du_i}{dt} = \Big[a_i(t) - \sum_{j=1}^{N} b_{ij}(t)u_j\Big]u_i, \quad i = 1, \ldots, N. \tag{3.1}$$

(The coefficients are always assumed to be bounded, continous, and nonnegative.) If the coefficients a_i and b_{ii} are bounded below by positive constants then the natural extension of condition (2.14) to the N-species case is

$$\inf a_i > \sum_{\substack{j=1 \\ j\neq i}}^{N} (\sup b_{ij})(\sup a_j)/\inf(b_{jj}), \quad i = 1 \ldots N. \tag{3.2}$$

A somewhat weaker condition is

$$\inf a_i \geq \sum_{\substack{j=1 \\ j\neq i}}^{N} (\sup b_{ij}) \sup(a_j/b_{jj}), \quad i = 1, \ldots N. \tag{3.3}$$

In [5], Professor Lazer and S. Ahmad proved

Theorem 3.1 *If the coefficients a_i, b_{ii} are bounded below by positive constants and (3.3) holds, then (3.1) has a unique solution $\vec{u}_*(t)$ such that*

$$0 < \inf_{t\in\mathbb{R}} u_{*i}(t) \leq \sup_{t\in\mathbb{R}} u_{*i}(t) < \infty, \tag{3.4}$$

and if $\vec{u}$ is any solution to (3.1) with $u_i(t_0) > 0$, $i = 1, \ldots, N$, for some t_0, then

$$|\vec{u}_*(t) - \vec{u}(t)| \to 0 \quad as \quad t \to \infty. \tag{3.5}$$

Remarks: The corresponding result for the periodic case under condition (3.2) was treated by Alvarez and Tineo [38]; the almost-periodic case with $N = 2$ by Ahmad [1]. This line of research was initiated by Gopalsamy [17,18], but his results required additional conditions. Theorem 3.1 is significant in part because it allows general time dependence. Many abstract results on persistence are set in the context of autonomous systems whose forward orbits are precompact; (see [21]). Even if a time dependent system is rewritten as an autonomous system by casting it as a skew product flow (see [35]), the forward orbits will not be precompact unless the time dependence is almost periodic. Thus Theorem 3.1 applies to systems where the abstract results discussed in [21] fail.

Condition (3.2) is an inequality between uniform bounds on coefficients of (3.1). Condition (3.3) is weaker than (3.2) because in (3.3) the quotient of uniform bounds, $\sup a_j / \inf b_{jj}$, is replaced by the uniform bound on the quotient $\sup(a_j/b_{jj})$. It is natural to ask whether the condition can be weakened further, perhaps to a condition imposing only a single uniform bound on some combination of coefficients of (3.1), or perhaps to some type of pointwise or average condition. It turns out that some such extensions are possible, but the issue is quite delicate. Suppose that in (3.1) we have $a_i, b_{ii} > 0$ and $\sup_{\mathbb{R}}(a_i/b_{ii}) < \infty$ for $i = 1, \ldots, N$ but do not assume that $\inf a_i > 0$ or that $\inf b_{ii} > 0$. Suppose further that

$$\inf_{\mathbb{R}} \left(\frac{a_i - \sum_{\substack{j=1 \\ j \neq i}}^{N} b_{ij} \sup(a_j/b_{jj})}{b_{ii}} \right) > 0 \tag{3.6}$$

and

$$\int_0^\infty b_{ii}(t)dt = \infty \tag{3.7}$$

for $i = 1, \ldots, N$.

Theorem 3.2 (Lazer and Ahmad [5]) *If (3.6) and (3.7) hold then any solution $\vec{u}(t)$ with $u_i(t_0) > 0$ for $i = 1, \ldots, N$ satisfies*

$$0 < \inf_{t > t_0} u_i(t) < \sup_{t > t_0} u_i(t) < \infty. \tag{3.8}$$

Furthermore, (3.1) has a solution $\vec{u}_*(t)$ satisfying (3.4).

Remarks: The solution $\vec{u}_*(t)$ may not be unique and thus the convergence property (3.5) may fail. A counterexample for the case $N = 6$ has been given by Redheffer [33,34]. Whether (3.6) and (3.7) imply uniqueness of $\vec{u}_*(t)$ and the convergence in (3.5) for $N \leq 5$ appears to be an open question. Other results related to those of [5] are also discussed in [33,34].

If solutions to (3.1) need not converge to a unique steady state $\vec{u}_*(t)$, what can be said about their asymptotic behavior? In general, competition systems can have arbitrarily complicated dynamics; see [36]. The conclusion (3.8) implies a version of strong persistence, so that species which are present initially will not become extinct, but that does not imply convergence. The answer is given in the following result:

Theorem 3.3 (Lazer and Ahmad [8]) *Suppose that* $a_i, b_{ii} > 0$ *and* $\sup(a_i/b_{ii}) < \infty$ *for* $i = 1, \ldots, N$, *and that (3.6) and (3.7) are satisfied. For* $A \subseteq ([0,\infty))^N \subseteq \mathbb{R}^N$ *define* $U(t, t_0, A) = \{\vec{u}(t) : \vec{u}(t_0) \in A, \vec{u}$ *satisfies* $(3.1)\}$. *If* $A \subseteq ((0,\infty))^N$ *is a bounded measurable set then* $\mu(U(t, t_0, A)) \to 0$ *as* $t \to \infty$, *where* μ *denotes* N*-dimensional Lebesgue measure.*

Remarks: Theorem 3.3 implies that although conditions (3.6) and (3.7) do not necessarily imply that solutions to (3.1) converge to a unique globally bounded solution, trajectories must converge in some generalized sense, because the system (3.1) takes sets of arbitrarily large finite measure and "squeezes" the measure toward zero as $t \to \infty$.

Persistence and Extinction in Nonautonomous Systems: Average Conditions

The conditions (3.6) and (3.7) are weaker than (3.2), essentially because they do not require uniform lower bounds on the coefficients a_i and b_{ii} in (3.1). However, (3.6) imposes a uniform lower bound on a combination of coefficients of (3.1). A different sort of generalization would replace uniform conditions with some type of average conditions. Suppose that $g(t)$ is a bounded continuous function on $\mathbb{R}$. The average of $g(t)$ on the interval t_1, t_2 is

$$A[g, t_1, t_2] = \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} g(s)ds.$$

The upper and lower averages of g on $\mathbb{R}$ are defined (respectively) as

$$M[g] = \limsup_{s\to\infty} \{A[g, t_1, t_2] : t_2 - t_1 > s\}$$

and

$$m[g] = \liminf_{s\to\infty} \{A[g, t_1, t_2] : t_2 - t_1 > s\}. \tag{3.10}$$

(If $g(t)$ is periodic or even almost periodic then $m[g] = M[g]$ and g has an average on $\mathbb{R}$.) Suppose that the coefficients a_i and b_{ii} in (3.1) are uniformly bounded below by positive constants. The condition analogous to (3.2) is then

$$m[a_i] \geq \sum_{\substack{j=1 \\ j\neq i}}^{N} \left(\sup_{\mathbb{R}} b_{ij}\right) M[a_j] / \left(\inf_{\mathbb{R}} b_{jj}\right), \quad i = 1, \ldots, N. \tag{3.11}$$

Theorem 3.4: (Lazer and Ahmad [9]): If (3.11) holds then for any solution of (3.1) with $u_i(t_0) > 0$ for $i = 1, \ldots, N$, (3.8) holds. If $\vec{u}$ and $\vec{v}$ are two componentwise positive solutions of (3.1), $\lim_{t\to\infty} |\vec{u}(t) - \vec{v}(t)| = 0$.

Remarks: Recall that (3.8) is a version of strong persistence. In this case the convergence result is stronger than in Theorem 3.3. The upper and lower averages satisfy $\inf_{\mathbb{R}}(g) \leq m[g] \leq M[g] \leq \sup_{\mathbb{R}}(g)$, so (3.2) implies (3.11). Theorem

3.4 is important because it gives a criterion for persistence even if populations experience occasional significant declines in their growth rates. Many populations are subject to serious but temporary declines in population growth rates because of sporadic events such as epidemics, periods of unfavorable weather, etc., so persistence results which can accomodate such phenomena are highly desirable for the study of natural systems.

It is of interest to know when populations can be expected to persist, but it is also important to be able to decide when a species faces extinction. In the case of two competitors and constant coefficients in (3.1), the second competitor will be forced to extinction by the first competitor (i.e. competitive exclusion will occur) if $a_1 > b_{12}a_2/b_{22}$ and $a_2 < b_{21}a_1/b_{11}$. This result was extended to the nonautonomous case under the condition $\inf a_1 > (\sup b_{12})(\sup a_2)/\inf(b_{22})$, $\sup a_2 < (\inf b_{21})(\inf a_1)/\sup(b_{11})$ by S. Ahmad [2]. In collaboration with Ahmad, Professor Lazer extended these results to criteria for the extinction of the Nth species (and the persistence of all other species) in models for N species. They treated the autonomous case in [6] and the specific nonautonomous case where the growth rates a_i depend on t but the other coefficients of (3.1) do not in [7]. Since the results of [7] imply those of [6],only they will be presented here. The first condition which is required is that the upper and lower averages (as defined in (3.9) and (3.10)) are equal for each of the coefficients a_i, so that each coefficient a_i has an average which is equal to $M[a_i]$. The second condition is that the first $N-1$ inequalities in (3.2) are satisfied, i.e. (3.2) holds for $i = 1, \ldots, N-1$. That condition implies the system of $N-1$ linear equations

$$M[a_i] = \sum_{j=1}^{N-1} b_{ij} x_j, \ i = 1, \ldots, N-1 \tag{3.12}$$

has a unique componentwise positive solution $x_i = \xi_i, \ i = 1 \ldots N-1$. (See [7].)

Theorem 3.4 (Lazer and Ahmad [7]) *Suppose that the coefficients a_i all have averages $M[a_i]$ and that the first $N-1$ inequalities of (3.2) are satisfied. Let $(\xi_1, \ldots, \xi_{N-1})$ be the unique componentwise positive solution to (3.12).*

i) If

$$M[a_N] < \sum_{j=1}^{N-1} b_{Nj}\xi_j \tag{3.13}$$

then for any solution of (3.1) with componentwise positive initial data, $u_N(t) \to 0$ as $t \to \infty$.

ii) If

$$M[a_N] > \sum_{j=1}^{N-1} b_{Nj}\xi_j \tag{3.14}$$

and $\vec{u}$ is a solution to (3.1) which is componentwise positive at $t = t_0$, then $\inf_{t>t_0} u_i(t) > 0$ for $i = 1, \ldots, N$.

iii) If

$$M[a_N] = \sum_{j=1}^{N-1} b_{N_j} \xi_j$$

then for any componentwise positive solution to (3.1), $\liminf_{t\to\infty} u_N(t) = 0$.

Remarks: Theorem 3.5 implies that if the first $N-1$ inequalities of (3.2) hold then (3.15) is necessary and sufficient for the conclusion that for solutions that are componentwise positive at $t = t_0$, $\inf_{t>t_0} u_i(t) > 0$ for $i = 1, \ldots, N$. It is also shown in [7] that if the only coefficients of (3.1) which vary in time are $a_i, i = 1, \ldots, N$, and the first $N-1$ inequalities in (3.2) are satisfied, and (3.13) holds, the (3.1) has a unique solution $\vec{u}_*(t) = (u_{1*}(t), \ldots, u_{N-1*}(t), 0)$ satisfying $0 < \inf_{\mathbb{R}} u_{i*}(t) \leq \sup_{\mathbb{R}} u_{i*}(t) < \infty$, and $\vec{u}_*(t)$ is globally asymptotically stable in the sense that $\lim_{t\to\infty} |\vec{u}_*(t) - \vec{u}(t)| = 0$ for any componentwise positive solution $\vec{u}(t)$. Some related results on extinction have been obtained by Montes de Oca and Zeeman [30], and conclusions about extinction in diffusive Lotka-Volterra models can be obtained via the methods of [13]. However, there has been much less research on conditions for extinction than on conditions for persistence, so the work contained in and inspired by [6,7] constitutes one important contribution to the literature.

Traveling Wavefronts in Diffusion Models

One of the more interesting and important properties of reaction-diffusion equations and systems is that they may support traveling wave solutions; see for example [37]. A traveling wave solution is simply a solution $\vec{u}(x,t) = \vec{u}(x+ct)$ which propagates a fixed profile at a fixed speed. To find traveling wave solutions one typically substitues $\vec{u} = \vec{\theta}(x+ct)$ into the reaction-difussion system and obtains a system of ordinary differential equations for $\vec{\theta}$ with c appearing as a parameter. If that system of ordinary differential equations has the right sort of solutions, those solutions yield traveling waves when $x + ct$ is used as the independent variable. For a single reaction-diffusion equation, the system of ordinary differential equations which determined the traveling waves consists of only two equations, so solutions leading to traveling waves can often be constructed by keeping track of how the phase plane for the system changes as the wavespeed parameter c is varied. For reaction-diffusion systems with two or more equations matters typically become much more delicate. Construction of traveling waves for systems may require a careful analysis of a higher dimensional phase space or may require the use of sophisticated methods such as the Conley index. It is remarkable that Professor Lazer and S. Ahmad [4] were able to give an elementary construction for travelling wavefronts in a class of systems which include some diffusive Lotka-Volterra models with many competitors. The specific systems that were treated in [4] are of the form

$$\frac{\partial u_i}{\partial t} = d_i \frac{\partial^2 u_i}{\partial x^2} + u_i f_i(\vec{u}), \quad i = 1, \ldots, N. \tag{3.15}$$

Theorem 3.6 (Lazer and Ahmad [4]) Suppose that the functions f_i in (3.15) are locally Lipschitz. Suppose that the system (3.15) admits a spatially constant equilibrium $\vec{a} = (a_1, \ldots, a_N)$ (so that $f_i(\vec{a}) = 0, \ \ i = 1 \ldots N$) such that

$$f_i(\vec{0}) \geq f_i(\vec{u}) > 0 \quad \text{if} \quad 0 \leq u_i \leq a_i \quad \text{for} \quad i = 1 \ldots N, \ \vec{u} \not\equiv \vec{a}. \tag{3.16}$$

Let $r_i = f_i(0)$. If

$$c^2 > 4 r_i d_i \tag{3.17}$$

then (3.15) has a wavefront solution $\vec{u} = \vec{\theta}(x + ct)$ of speed c with $\vec{\theta}(s) \to \vec{0}$ as $s \to \infty, \ \vec{\theta}(s) \to \vec{a}$ as $s \to -\infty$.

Sketch of Proof: A traveling wave solution satisfies the system

$$d_i \theta_i'' = -c\theta_i' - \theta_i f_i(\vec{\theta}), \ \ i = 1 \ldots N. \tag{3.18}$$

The hypothesis (3.17) implies that there exist numbers μ_i so that $\mu_i^2 - (c/d_i)\mu_i + (r_i/d_i) < 0$. The proof proceeds as follows:

1) Show that the set $0 < \theta_i < a_i, \ -\mu_i\theta_i < \theta_i' < 0$ is positively invariant in the phase space of (3.18) via differential inequalities.

2) Show that the bounds in 1) imply that $\theta_i(s), \theta_i'(s) \to 0$ as $s \to \infty$ (multiply (3.18) by θ_i' and integrate).

3) Choose a sequence $\vec{\theta}_m^* = (\theta_{im}^*, \ldots, \theta_{Nm}^*)$ of functions satisfying (3.18) such that $\theta_{im}^*(0) = a_i, \ \theta_{im}^{*\prime}(0) = -\epsilon_m$, where $\epsilon_m \to 0$ as $m \to \infty$. Choose τ_m such that $\theta_{im}^*(\tau_m) \geq a_i/2$ for each i and $\theta_{jm}^*(\tau_m) = a_j/2$ for some j. Show that $\tau_m \to \infty$ as $m \to \infty$ by using the continuous dependence of solutions on initial data.

4) Let $\theta_{im}(s) = \theta_{im}^*(s + \tau_m)$ and show that $\vec{\theta}_m(s) \to \vec{\theta}(s)$ for a subsequence of $\{\theta_m\}$ by arguments based on continuous dependence on initial data and compactness.

Remarks: All of the steps in the analysis are elementary.

4 Conclusions

The results and ideas described in the earlier sections of this article show the scope and depth of Professor Lazer's contributions to mathematical propulation dynamics. His work has introduced fundamental new results, methods, and ideas into the study of time dependent population models, among other areas. For applied purposes it is important to be able to treat time dependent population models, because natural populations are very often influenced by factors which vary in time. Those factors include daily and seasonal variations, in things such as temperature and light which are at least approximately periodic, but they also include factors such as rainfall which are less regular and predictable. Thus, both periodic and nonperiodic variations are important to consider. Another important feature of much of Professor Lazer's work is that he has often been able to obtain deep results via relatively elementary methods. This feature makes his work accessible to a wide range of scientists. Finally, Professor Lazer has inspired many collaborators, students, colleagues, and other mathematical acquaintances. A few of those have been mentioned here by name, but many others have not. Through his own work and his influence on others, Professor Lazer's contributions to mathematical population dynamics have permanently changed that subject.

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