Ensemble and Trajectory Statistics in a Nonlinear Partial Differential Equation

Michael C. Mackey,¹ and Helmut Schwegler²

We have examined the influence of parametric noise on the solution behavior u(t, x) of a nonlinear initial value (φ) problem arising in cell kinetics. In terms of ensemble statistics, the eventual limiting solution mean ξ_u and variance $\bar{\sigma}_u^2$ are well-characterized functions of the noise statistics, and ξ_u and $\bar{\sigma}_u^2$ depend on φ . When noise is continuously present along the trajectory, ξ_u and $\bar{\sigma}_u^2$ are independent of the noise statistics and φ . However, in their evolution toward ξ_u and $\bar{\sigma}_u^2$, both $\xi_u(t, x)$ and $\sigma_u^2(t, x)$ depend on the noise and φ .

KEY WORDS: Parametric noise; nonlinear partial differential equations; ensemble statistics; trajectory statistics.

1. INTRODUCTION

Many biological populations are *age structured* in that the recruitment of new individuals into the population depends on the density of a cohort of older individuals, e.g., all mammalian populations and populations of replicating and maturing cells. Models of these age-structured populations are most naturally framed in terms of first-order partial differential equations ("transport-like" equations) that are often nonlinear because of dependences of birth and/or death rates on population number (see Metz and Diekmann⁽¹⁾ for an excellent survey).

Over the past decade a variety of mathematical results illustrating the solution stability, and sometimes sensitive dependence of the solution behavior to the initial function, of these age-structured population models have appeared,⁽²⁻⁸⁾ but they are not generally known in the broader

281

¹ Departments of Physiology, Physics and Mathematics and Center for Nonlinear Dynamics, McGill University, Montreal, Canada H3G 1Y6.

² Institute of Theoretical Physics, University of Bremen, D-2800 Bremen, Germany.

community. This paper illustrates these results using a nonlinear equation motivated by a simple model for cellular replication and maturation, and then examines the effect of parametric noise on the eventual solution behavior of the model.

The plan of the paper is as follows. Section 2 summarizes some of the recent mathematical results of Lasota.⁽⁴⁾ Section 3 illustrates the significance of these results using a simple, analytically tractable, nonlinear transport equation. We then examine the effect of parametric noise in Sections 4 and 5.

2. MATHEMATICAL PRELIMINARIES

There are several interesting results concerning the solution behavior of first-order partial differential equations with respect to stability and exactness.⁽²⁻⁸⁾ Most of this work was initiated by the work of Lasota,⁽⁴⁾ who considers the partial differential equation

$$\frac{\partial u}{\partial t} + c(t, x) \frac{\partial u}{\partial x} = f(t, x, u) \quad \text{for} \quad (t, x) \in D$$
 (1)

with the initial condition

$$u(0, x) = \varphi(x) \quad \text{for} \quad x \in \Delta$$
 (2)

This section summarizes those results.

In (1) and (2), $\Delta = [0, 1]$, $D = [0, \infty) \times \Delta$, and c, f are continuously differentiable functions satisfying the following conditions:

$$c(t, x) \ge 0$$
 for $(t, x) \in D$ (3a)

$$f(t, x, u) \ge 0$$
 for $(t, x) \in D$ (3b)

$$f(t, x, u) \leq k_1(t)u + k_2(t)$$
 for $(t, x) \in D, u \geq 0$ (3c)

with continuous coefficients k_1 , k_2 . We also let $C_+(A)$ be the set of all nonnegative continuously differentiable functions defined on the set A.

The first result is related to the uniqueness of the solution of Eq. (1) with (2).

Theorem 1. If c and f satisfy inequalities (3) and

$$c(t,0) = 0 \qquad \text{for} \quad t \ge 0 \tag{4}$$

then for each $\varphi \in C_+(\Delta)$ Eqs. (1) and (2) have a unique solution $u \in C_+(D)$. Conversely, if for one $\varphi \in C_+(\Delta)$ Eqs. (1) and (2) have a unique solution $u \in C_+(D)$, then c satisfies (4).

Before stating a stability result, we require a further set of conditions, namely that

$$c(t, x) \ge c_0(x) > 0$$
 for $(t, x) \in D, x > 0$ (5a)

$$\frac{f(t, x, u)}{u - u_0} \leqslant f_0(x, u) \qquad \text{for} \quad (t, x) \in D, \quad u \neq u_0 \tag{5b}$$

where $u \ge u_0 > 0$ is a given number, c_0 is a continuous function, and f_0 is a continuous bounded function such that

$$f_0(x, 0) \le 0, \quad f_0(0, u) < 0 \quad \text{for } x \in \Delta, \quad u > 0$$
 (5c)

Then we have the following result.

Theorem 2. If c and f satisfy conditions (4) and (5), then for each $\varphi \in C_+(\Delta)$ such that $\varphi(0) > 0$ the solution of Eqs. (1) and (2) satisfies

$$\lim_{t \to \infty} u(t, x) = u_0 \qquad \text{uniformly for} \quad x \in \Delta \tag{6}$$

The next results are concerned only with the autonomous case of Eqs. (1) and (2), so we consider

$$\frac{\partial u}{\partial t} + c(x)\frac{\partial u}{\partial x} = f(x, u) \quad \text{for} \quad (t, x) \in D$$
 (7)

with the initial condition

$$u(0, x) = \varphi(x)$$
 for $x \in \Delta$ (8)

Both c and f are assumed to be continuously differentiable as before, and we also assume that

$$c(0) = 0, \quad c(x) > 0 \quad \text{for} \quad 0 < x \le 1$$
 (9a)

$$f_u(0, u_0) < 0, \qquad f(0, u)(u - u_0) < 0 \qquad \text{for} \quad u > 0, \quad u \neq u_0 > 0 \quad (9b)$$

and

$$0 \leq f(x, 0), \quad f(x, u) \leq k_1 u + k_2 \quad \text{for } x \in \Lambda, \quad u \geq 0$$
 (9c)

with constant k_1 , $k_2 > 0$.

Theorem 3. If c and f satisfy conditions (9), then for all initial functions φ such that $\varphi(0) > 0$ with $\varphi \in C_+(\Delta)$ the solution u of Eqs. (7) and (8) satisfies

$$\lim_{t \to \infty} u(t, x) = w_0(x) \qquad \text{uniformly for } x \in \Delta \tag{10}$$

where $w_0(x)$, which is continuous for $x \in \Delta$ and differentiable for $0 < x \le 1$, is the unique solution of the initial value problem

$$c(x)\frac{dw}{dx} = f(x, w), \qquad 0 < x \le 1, \quad w(0) = u_0 \tag{11}$$

To appreciate what happens when the solution u of (1)-(2) is not stable, we introduce a bit of terminology. Consider the solutions of Eqs. (7) and (8) as the trajectories of the semidynamical system $\{S_t\}_{t\geq 0}$ defined by

$$(S_t \varphi)(x) = u(t, x)$$

where u(t, x) is the solution of Eqs. (7) and (8). Each S_t is a continuous mapping of $C_+(\Delta)$ into itself and

$$S_0 \varphi = \varphi,$$
 $S_{t_1}(S_{t_2}\varphi) = S_{t_1+t_2}\varphi$ for $t_1, t_2 \ge 0, \varphi \in C_+(\varDelta)$

We further define two sets of functions

$$\Xi_0 = \{ \varphi \in C_+(\varDelta) \colon \varphi(0) = 0 \}$$

and

$$\Xi_w = \{ \varphi \in \Xi_0 : \varphi(x) < w_0(x) \text{ for } x \in \varDelta \}$$

Given an arbitrary metric space Ξ and an arbitrary semidynamical system $\{S_t\}_{t\geq 0}$ operating on Ξ , a point $\varphi \in \Xi$ is called *stable* if for any sequence $\varphi_n \in \Xi$ the condition $\lim_{n\to\infty} \varphi_n = \varphi$ implies that $S_t \varphi_n \to S_t \varphi$ uniformly for all $t\geq 0$. The system $\{S_t\}$ is called *chaotic* if: (a) every point $\varphi \in \Xi$ is unstable; and (b) there exists $\varphi \in \Xi$ such that the trajectory $\{S_t\varphi: t\geq 0\}$ is dense in Ξ .

Now we have the following most interesting result.

Theorem 4. If the functions c and f satisfy conditions (9) and

$$f(0,0) = 0 \tag{12}$$

then the semidynamical system $\{S_t\}_{t\geq 0}$ generated by the initial value problem of Eqs. (7) and (8) is chaotic in the set Ξ_w .

3. A SIMPLE EXAMPLE

To illustrate these results, we turn to a mathematical formulation of a model for a renewing and maturing cellular population.⁽⁹⁻¹¹⁾ Let u(t, x) be the number of cells of age x at time t, where the finite age x is normalized

so $x \in [0, 1]$. Then the function u can be shown to obey the first-order partial differential equation

$$\frac{\partial u}{\partial t} + rx \frac{\partial u}{\partial x} = \alpha u (1 - u) \tag{13}$$

with the associated initial condition

$$u(0, x) = \varphi(x) \tag{14}$$

In (13), rx (with r > 0) is the velocity of aging and $\alpha \in R$ is a constant related to the relative proliferation rate and the cell death rate.

Using the method of characteristics, the general solution to Eq. (13) with (14) is given by

$$u(t, x) = \frac{\varphi(xe^{-rt})e^{\alpha t}}{1 - \varphi(xe^{-rt})[1 - e^{\alpha t}]}$$
(15)

Having this analytic solution allows us to clearly demonstrate all of the interesting aspects of the results quoted in Section 2.

First note that since all of the conditions of Theorem 1 are satisfied, the solution given by Eq. (15) is unique. Second, in considering the stability of (15), note that conditions (9) are easily shown to be satisfied for α both positive and negative (but not for $\alpha = 0$).³ As a consequence, as long as $\varphi(0) > 0$, the solution (15) is globally stable by Theorem 3, and in fact

$$\lim_{t \to \infty} u(t, x) = \begin{cases} 0, & \alpha < 0\\ 1, & 0 < \alpha \end{cases}$$
(16)

However, if $\varphi(0) = 0$, the solutions (15) are chaotic in the sense of Theorem 4, since (13) satisfies (12). This can be demonstrated by picking an initial function of the form

$$\varphi(y) = \beta y^n \quad \text{for} \quad y \in \Delta = [0, 1], \quad \beta \in (0, 1) \tag{17}$$

Then (15) takes the explicit form

$$u(t, x) = \frac{\beta x^n e^{(\alpha - nr)t}}{1 - \beta x^n e^{-nrt} + \beta x^n e^{(\alpha - nr)t}}$$
(18)

from which

$$\lim_{t \to \infty} u(t, x) = \begin{cases} 0, & \alpha < nr \\ \frac{\beta x^n}{1 + \beta x^n}, & nr = \alpha \\ 1, & nr < \alpha \end{cases}$$
(19)

³ When $\alpha = 0$, the solution of (13) is $u(t, x) = \varphi(xe^{-t})$ and $\lim_{t \to \infty} u(t, x) = \varphi(0)$.

This analytic solution (19) explicitly demonstrates the multistability that may be exhibited by the "chaotic" solutions (15) of (13) when $\varphi(0) = 0$. Namely, depending on which initial function φ is drawn from the class Ξ_w of initial functions (see Theorem 4), the solution (15) will, in the long-time $(t \to \infty)$ limit, be uniformly 0 or 1 or show spatial dependence. Thus, in a fashion entirely analogous to discrete- and continuous-time chaotic systems, the solution u displays a sensitive dependence on the initial condition (i.e., on the initial function φ).

4. ENSEMBLE STATISTICS

In this section we examine how the dynamics of Eq. (13) discussed in the previous section would be manifested in the statistics of an ensemble. We assume that each unit in the ensemble has dynamics described by (13), but each has a different value of the parameter α . Specifically, α is assumed to be distributed with density $g(\alpha)$ for $\bar{\alpha} - \Delta \alpha \leq \alpha \leq \bar{\alpha} + \Delta \alpha$.

For illustrative purposes, and to allow the required moments of u to be calculated analytically, assume that the density g of the distribution of α values is the rectangular (uniform) density

$$g(\alpha) = \begin{cases} 1/(2\Delta\alpha), & \bar{\alpha} - \Delta\alpha \leqslant \alpha \leqslant \bar{\alpha} + \Delta\alpha \\ 0, & \text{otherwise} \end{cases}$$
(20)

The mean value of α is

$$\xi_{\alpha} = \int_{\bar{\alpha} - \Delta\alpha}^{\bar{\alpha} + \Delta\alpha} \alpha g(\alpha) \, d\alpha = \bar{\alpha} \tag{21}$$

while the variance is

$$\sigma_{\alpha}^{2} = \int_{\bar{\alpha} - \Delta\alpha}^{\bar{\alpha} + \Delta\alpha} \left[\alpha - \zeta_{\alpha} \right]^{2} g(\alpha) \, d\alpha = \frac{(\Delta\alpha)^{2}}{3} \tag{22}$$

The mean value

$$\xi_u(t, x) = \langle u(t, x) \rangle = \int_{\tilde{\alpha} - \Delta \alpha}^{\tilde{\alpha} + \Delta \alpha} u(t, x) g(\alpha) \, d\alpha$$

of u across the entire ensemble is given by averaging (15), weighted by the uniform density (20):

$$\xi_{u}(t,x) = \frac{1}{2t \, \Delta\alpha} \ln \left\{ \frac{\varphi(xe^{-rt}) \, e^{(\bar{\alpha} + \Delta\alpha)t} + 1 - \varphi(xe^{-rt})}{\varphi(xe^{-rt}) \, e^{(\bar{\alpha} - \Delta\alpha)t} + 1 - \varphi(xe^{-rt})} \right\}$$
(23)

Further, the mean square of u is

$$\langle u^{2}(t, x) \rangle = \int_{\bar{\alpha} - \Delta\alpha}^{\bar{\alpha} + \Delta\alpha} u^{2}(t, x) g(\alpha) \, d\alpha$$
$$= \langle u(t, x) \rangle + R(t, x)$$
(24)

where

$$R(t, x) = \frac{1 - \varphi(xe^{-rt})}{2t \, \Delta \alpha} \left\{ \frac{1}{\varphi(xe^{-rt}) \, e^{(\tilde{\alpha} + \Delta \alpha)t} + 1 - \varphi(xe^{-rt})} - \frac{1}{\varphi(xe^{-rt}) \, e^{(\tilde{\alpha} - \Delta \alpha)t} + 1 - \varphi(xe^{-rt})} \right\}$$
(25)

so the variance of u, $\sigma_u^2(t, x) = \langle u^2(t, x) \rangle - \langle u(t, x) \rangle^2$, is given by

$$\sigma_u^2(t,x) = \langle u(t,x) \rangle [1 - \langle u(t,x) \rangle] + R(t,x)$$
(26)

To understand the effects of this distribution of α across the ensemble, we examine the long-time limits of ξ_u and σ_u^2 , noting that $\lim_{t\to\infty} R(t, x) = 0$.

The Case of \varphi(0) > 0. When $\varphi(0) > 0$, the mean value ξ_u has the following limiting values:

$$\bar{\xi}_{u} \equiv \lim_{t \to \infty} \xi_{u} = \begin{cases} 0, & \bar{\alpha} \leqslant -\Delta\alpha \\ \frac{\bar{\alpha} + \Delta\alpha}{2\Delta\alpha}, & -\Delta\alpha \leqslant \bar{\alpha} \leqslant \Delta\alpha \\ 1, & \Delta\alpha \leqslant \bar{\alpha} \end{cases}$$
(27)

and the limiting variance is

$$\bar{\sigma}_{u}^{2} \equiv \lim_{t \to \infty} \sigma_{u}^{2} = \begin{cases} 0, & \bar{\alpha} \leqslant -\Delta\alpha \\ -\frac{(\bar{\alpha} - \Delta\alpha)(\bar{\alpha} + \Delta\alpha)}{2\Delta\alpha}, & -\Delta\alpha \leqslant \bar{\alpha} \leqslant \Delta\alpha \\ 0, & \Delta\alpha \leqslant \bar{\alpha} \end{cases}$$
(28)

From (21) and (22) it is straightforward to rewrite (27) in terms of the mean and standard deviation of α across the ensemble:

$$\bar{\xi}_{u} = \begin{cases} 0, & \frac{\xi_{\alpha}}{\sqrt{3}\sigma_{\alpha}} \leqslant -1 \\ \frac{1}{2} \left(1 + \frac{\xi_{\alpha}}{\sqrt{3}\sigma_{\alpha}} \right), & -1 \leqslant \frac{\xi_{\alpha}}{\sqrt{3}\sigma_{\alpha}} \leqslant 1 \\ 1, & 1 \leqslant \frac{\xi_{\alpha}}{\sqrt{3}\sigma_{\alpha}} \end{cases}$$
(29)

Similarly, the long-time limiting variance can be rewritten as

$$\bar{\sigma}_{u}^{2} = \begin{cases} 0, & \frac{\xi_{\alpha}}{\sqrt{3}\sigma_{\alpha}} \leqslant -1 \\ \frac{\sqrt{3}\sigma_{\alpha}}{2} \left[1 - \left(\frac{\xi_{\alpha}}{\sqrt{3}\sigma_{\alpha}}\right)^{2} \right], & -1 \leqslant \frac{\xi_{\alpha}}{\sqrt{3}\sigma_{\alpha}} \leqslant 1 \\ 0, & 1 \leqslant \frac{\xi_{\alpha}}{\sqrt{3}\sigma_{\alpha}} \end{cases}$$
(30)

Several aspects of these simple forms for $\bar{\xi}_u$ and $\bar{\sigma}_u^2$ as functions of $\xi_{\alpha}/\sqrt{3} \sigma_{\alpha}$ are striking. First, the different limiting values exhibited in (16) have been replaced by a continuum of $\bar{\xi}_u$ values in the ensemble ranging from $\bar{\xi}_u = 0$ for $\xi_{\alpha}/\sqrt{3} \sigma_{\alpha} \leq -1$, through a continuous increase in $\bar{\xi}_u$ from 0 to 1 for $-1 \leq \xi_{\alpha}/\sqrt{3} \sigma_{\alpha} \leq 1$, to finally culminate in $\bar{\xi}_u = 1$ for $1 \leq \xi_{\alpha}/\sqrt{3} \sigma_{\alpha}$. These behaviors are an obvious extension of the limits in (16) when it is realized that $\xi_{\alpha}/\sqrt{3} \sigma_{\alpha} \leq -1$ corresponds to $\bar{\alpha} + \Delta \alpha = 0$, while $1 \leq \xi_{\alpha}/\sqrt{3} \sigma_{\alpha}$ is equivalent to $\bar{\alpha} - \Delta \alpha = 0$. Second, it is only for $-1 < \xi_{\alpha}/\sqrt{3} \sigma_{\alpha} < 1$ that the limiting variance $\bar{\sigma}_u^2$ is nonzero, and it has a maximum of $(\sqrt{3} \sigma_{\alpha})/2$ when $\xi_{\alpha}/\sqrt{3} \sigma_{\alpha} \equiv 0$. Finally, from an ensemble perspective changes in the standard deviation σ_{α} have an anomalous effect depending on the sign of ξ_{α} . Namely, for $\xi_{\alpha} > 0$, decreasing σ_{α} drives $\bar{\xi}_u$ toward its maximum of 0.

The Case of $\varphi(0) = 0$. When $\varphi(0) = 0$, and specifically for the initial function (17), the mean ξ_{μ} has the following limits:

$$\bar{\xi}_{u} = \begin{cases} 0, & \bar{\alpha} \leq nr - \Delta\alpha \\ \frac{\bar{\alpha} + \Delta\alpha - nr}{2\Delta\alpha}, & nr - \Delta\alpha \leq \bar{\alpha} \leq nr + \Delta\alpha \\ 1, & nr + \Delta\alpha \leq \bar{\alpha} \end{cases}$$
(31)

which are slightly different from the previous case. Further, the limiting variance is

$$\bar{\sigma}_{u}^{2} = \begin{cases} 0, & \bar{\alpha} \leq nr - \Delta \alpha \\ -\frac{(\bar{\alpha} - \Delta \alpha - nr)(\bar{\alpha} + \Delta \alpha - nr)}{2\Delta \alpha}, & nr - \Delta \alpha \leq \bar{\alpha} \leq nr + \Delta \alpha \\ 0, & nr + \Delta \alpha \leq \bar{\alpha} \end{cases}$$
(32)

Again rewriting $\bar{\alpha}$ and $\Delta \alpha$ in terms of ξ_{α} and σ_{α} , (31) and (32) become

$$\bar{\xi}_{u} = \begin{cases} 0, & \frac{\xi_{\alpha} - nr}{\sqrt{3} \sigma_{\alpha}} \leqslant -1 \\ \frac{1}{2} \left(1 + \frac{\xi_{\alpha} - nr}{\sqrt{3} \sigma_{\alpha}} \right), & -1 \leqslant \frac{\xi_{\alpha} - nr}{\sqrt{3} \sigma_{\alpha}} \leqslant 1 \\ 1, & 1 \leqslant \frac{\xi_{\alpha} - nr}{\sqrt{3} \sigma_{\alpha}} \end{cases}$$
(33)

and

$$\bar{\sigma}_{u}^{2} = \begin{cases} 0, & \frac{\xi_{\alpha} - nr}{\sqrt{3} \sigma_{\alpha}} \leqslant -1 \\ \frac{\sqrt{3} \sigma_{\alpha}}{2} \left[1 - \left(\frac{\xi_{\alpha} - nr}{\sqrt{3} \sigma_{\alpha}}\right)^{2} \right], & -1 \leqslant \frac{\xi_{\alpha} - nr}{\sqrt{3} \sigma_{\alpha}} \leqslant 1 \\ 0, & 1 \leqslant \frac{\xi_{\alpha} - nr}{\sqrt{3} \sigma_{\alpha}} \end{cases}$$
(34)

From (33) and (34), it is clear that the effect of having an initial function of the form (17) is to simply shift the graphs of ξ_u and σ_u versus $\xi_{\alpha}/\sqrt{3} \sigma_{\alpha}$ to the right by a factor of $nr/\sqrt{3} \sigma_{\alpha}$.

5. TRAJECTORY STATISTICS

In contrast to the previous section, we now examine the alterative situation in which the parameter α of Eq. (13) fluctuates along the trajectory as a function of time. Specifically, we assume that

$$\alpha = \bar{\alpha} + \frac{dw(t)}{dt}$$

wherein w is assumed to be a uniformly distributed Wiener process with density given by

$$g(w) = \begin{cases} 1/(2\Delta w), & -\Delta w \le w \le \Delta w \\ 0, & \text{otherwise} \end{cases}$$
(35)

The Wiener process w has a mean value

$$\xi_w = \int_{-\Delta w}^{\Delta w} wg(w) \, dw = 0 \tag{36}$$

and variance

$$\sigma_w^2 = \int_{-\Delta w}^{\Delta w} \left[w - \xi_w \right]^2 g(w) \, dw = \frac{(\Delta w)^2}{3} \tag{37}$$

We may once again solve Eq. (13) with the initial condition (14) using the method of characteristics, but realizing that the characteristic equation for u is no longer an ordinary differential equation. Rather, it is a stochastic differential equation, given by

$$\frac{du}{u(1-u)} = \bar{\alpha} \, dt + dw(t) \tag{38}$$

Interpreting (38) in the sense of the Ito calculus,⁽¹²⁾ we have the solution

$$u(t, x) = \frac{\varphi(xe^{-rt}) e^{\bar{\alpha}t} e^{w(t)}}{1 - \varphi(xe^{-rt}) [1 - e^{\bar{\alpha}t} e^{w(t)}]}$$
(39)

The mean value of u for a large number of realizations is

$$\xi_{u}(t,x) = \frac{1}{2\Delta w} \ln \left\{ \frac{\varphi(xe^{-rt}) e^{\tilde{\alpha}t} e^{\Delta w} + 1 - \varphi(xe^{-rt})}{\varphi(xe^{-rt}) e^{\tilde{\alpha}t} e^{-\Delta w} + 1 - \varphi(xe^{-rt})} \right\}$$
(40)

Further, the mean square of u once again satisfies (24) with

$$R(t, x) = \frac{1 - \varphi(xe^{-rt})}{2\Delta w} \left\{ \frac{1}{\varphi(xe^{-rt}) e^{\bar{\alpha}t}e^{\Delta w} + 1 - \varphi(xe^{-rt})} - \frac{1}{\varphi(xe^{-rt}) e^{\bar{\alpha}t}e^{-\Delta w} + 1 - \varphi(xe^{-rt})} \right\}$$
(41)

[again $\lim_{t\to\infty} R(t, x) = 0$], so the variance $\sigma_u^2(t, x)$ is given by (26) as before.

a. Limiting $(t \to \infty)$ Solution Statistics. The long-time limits of ξ_u and σ_u^2 show behavior quite different from the ensemble behavior. For $\varphi(0) > 0$, the mean value ξ_u has the limiting values

$$\bar{\xi}_{u} \equiv \lim_{t \to \infty} \xi_{u} = \begin{cases} 0, & \bar{\alpha} < 0\\ \frac{1}{2\Delta w} \ln \left\{ \frac{\varphi(0) e^{\Delta w} + 1 - \varphi(0)}{\varphi(0) e^{-\Delta w} + 1 - \varphi(0)} \right\}, & \bar{\alpha} = 0 \\ 1, & 0 < \bar{\alpha} \end{cases}$$
(42)

290

while the limiting variance is

$$\bar{\sigma}_{u}^{2} \equiv \lim_{t \to \infty} \sigma_{u}^{2} = \begin{cases} 0, & \bar{\alpha} < 0\\ \bar{\xi}_{u}(\bar{\alpha} = 0)[1 - \bar{\xi}_{u}(\bar{\alpha} = 0)], & 0 = \bar{\alpha}\\ 0, & 0 < \bar{\alpha} \end{cases}$$
(43)

These limits may be understood from the dynamics of the original equation. Since the noise on the parameter α was assumed to be additive, the noise *amplitude* will approach zero as $u \rightarrow 0$ or $u \rightarrow 1$. Consequently, the limiting mean values given by (42) coincide with either 0 or 1, which are the limiting values of u. Further, since the amplitude of the noise goes to zero in these two limiting cases, it is not unexpected that the limiting variance is zero. When φ is given by (17), so $\varphi(0) = 0$, the same conclusions hold if $\overline{\alpha}$ is replaced by $\overline{\alpha} - nr$.

b. Temporal Behavior of Solution Statistics. To more fully examine the effect of fluctuations in α on the statistics of the solution of (15), we turn to an examination of the temporal evolution of $\xi_u(t, x)$ and $\sigma_u^2(t, x)$ to their limiting values given in (42) and (43), respectively.

This is perhaps easiest if we assume the noise amplitude Δw is small and expand the expressions (40) and (41) in powers of Δw . Denote the solution (39) in the absence of noise ($\Delta w \equiv 0$) by u_0 , which is given by

$$u_0(t,x) = \frac{\varphi(xe^{-rt}) e^{\tilde{\alpha}t}}{1 - \varphi(xe^{-rt})[1 - e^{\tilde{\alpha}t}]}$$
(44)

Then a rather tedious calculation gives

$$\xi_{u}(t, x) \simeq u_{0}(t, x) \left\{ 1 + \frac{(\varDelta w)^{2}}{6} \left[1 - u_{0}(t, x) \right] \left[1 - 2u_{0}(t, x) \right] + \mathcal{O}((\varDelta w)^{4}) \right\}$$
$$= u_{0}(t, x) \left\{ 1 + \frac{\sigma_{u}^{2}}{2} \left[1 - u_{0}(t, x) \right] \left[1 - 2u_{0}(t, x) \right] + \mathcal{O}(\sigma_{w}^{4}) \right\}$$
(45)

Carrying out the same procedure for the factor R defined in (41), and then using the result plus (45) in the expression (26) for the variance, gives

$$\sigma_u^2(t, x) \simeq \frac{(\varDelta w)^2}{3} u_0^2(t, x) [1 - u_0(t, x)]^2 + \mathcal{O}((\varDelta w)^4)$$
$$= \sigma_w^2 u_0^2(t, x) [1 - u_0(t, x)]^2 + \mathcal{O}(\sigma_w^4)$$
(46)

Equations (45) and (46) show the origin of the limiting behavior of ξ_u and σ_u^2 displayed in (42) and (43). From (45) it follows that the sign of the

Mackey and Schwegler

term in $\sigma_w^2(t, x)$ will be positive for $0 < u_0(t, x) < 1/2$ and negative for $1/2 < u_0(t, x) < 1$. Consequently, $\xi_u(t, x)$ will be, respectively, greater or less than $u_0(t, x)$ in these circumstances. The maximum deviation of $\xi_u(t, x)$ away from $u_0(t, x)$ occurs when

$$u_0(t, x) = \frac{1}{2} \pm \frac{\sqrt{3}}{6}$$

To understand the effect of noise on the evolution of the variance (46), consider the following. The maximum variance occurs when $u_0(t, x) \equiv 1/2$ and has the value

$$\sigma_{u,\max}^2(t,x) = \frac{\sigma_w^2}{16}$$

We now pose the following question. What are the conditions such that

$$(1-\varepsilon)^2 \sigma_{u,\max}^2(t,x) \leq \sigma_u^2(t,x) \leq \sigma_{u,\max}^2(t,x)$$
(47)

where $\varepsilon \in [0, 1]$? Condition (47) is equivalent to

$$\frac{1-\sqrt{\varepsilon}}{2} \leqslant u_0(t,x) \leqslant \frac{1+\sqrt{\varepsilon}}{2}$$

A general discussion of when (47) is satisfied for all initial functions φ is quite complicated. We restrict ourselves to a few simple cases.

In the simplest case where $\varphi \equiv \mathscr{C}$ is a constant, then simple graphical considerations (Fig. 1a) indicate that the time *interval* $T_{\varepsilon}(x^*)$ over which σ_u^2 satisfies (47) will be maximized by picking

$$\mathscr{C} \leqslant \frac{1 - \sqrt{\varepsilon}}{2} \quad \text{for} \quad \bar{\alpha} > 0$$

$$\mathscr{C} \geqslant \frac{1 + \sqrt{\varepsilon}}{2} \quad \text{for} \quad \bar{\alpha} < 0$$
(48)

and that T_{ε} is a decreasing function of increasing $|\alpha|$ when conditions (48) are satisfied. If $\bar{\alpha} \equiv 0$, then it is trivial that (47) can be satisfied for all time if

$$\frac{1-\sqrt{\varepsilon}}{2} \leqslant \mathscr{C} \leqslant \frac{1+\sqrt{\varepsilon}}{2}$$

Things become more interesting in the case that $\varphi(0) = 0$, as can be illustrated (see Fig. 1b) with the initial function (17), so u_0 has the explicit solution

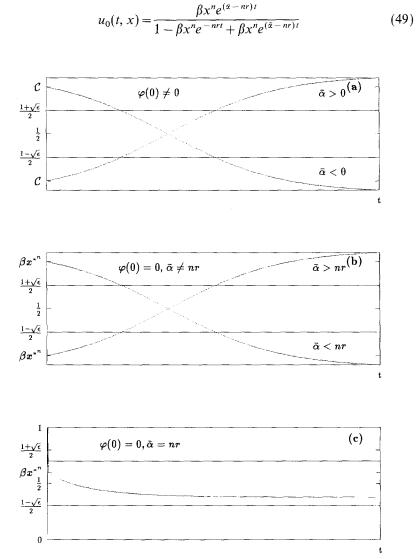


Fig. 1. Graphical illustration of the discussion of Eq. (47). (a) For a spatially constant initial function φ ; (b, c) for $\varphi(y) = \beta y^n$, so $\varphi(0) = 0$. (b) $\bar{\alpha} \neq nr$; (c) $\bar{\alpha} \equiv nr$. In the text discussion the duration T_{ε} is the length of time the noiseless solution $u_0(t, x)$ spends in the interval $[(1 - \sqrt{\varepsilon})/2]$, denoted by the horizontal dashed lines.

Mackey and Schwegler

Remember that $u_0(t=0, x) = \beta x^n$ and

$$\lim_{t \to \infty} u_0(t, x) = \begin{cases} 0, & \bar{\alpha} < nr \\ \frac{\beta x^n}{1 + \beta x^n}, & nr = \bar{\alpha} \\ 1, & nr < \bar{\alpha} \end{cases}$$
(50)

When $\bar{\alpha} \neq nr$, then for a given $x = x^*$ we can maximize the time $T_{\varepsilon}(x^*)$ over which (47) is satisfied by picking β such that

$$\beta \leqslant \frac{1 - \sqrt{\varepsilon}}{2} \frac{1}{x^{*n}} \quad \text{for} \quad \bar{\alpha} > nr$$

$$\beta \geqslant \frac{1 + \sqrt{\varepsilon}}{2} \frac{1}{x^{*n}} \quad \text{for} \quad \bar{\alpha} < nr$$
(51)

From graphical considerations we expect that the maximal value of $T_{\varepsilon}(x^*)$ should be a decreasing function of $|\bar{\alpha} - nr|$, and for small ε a simple calculation shows that

maximum
$$T_{\varepsilon}(x^*) \simeq \mathcal{O}\left(\frac{\sqrt{\varepsilon}}{|\bar{\alpha} - nr|}\right)$$

When $\bar{\alpha} \equiv nr$ the situation is somewhat different, as can be seen by examining the solution (49) in this situation:

$$u_0(t,x) = \frac{\beta x^n}{1 - \beta x^n e^{-nrt} + \beta x^n}$$
(52)

Noting that $u_0(t, x)$ is, in this case, a monotone decreasing function of time with

$$u_0(t=0, x) \equiv \beta x^n \ge \frac{\beta x^n}{1+\beta x^n} \equiv \lim_{t \to \infty} u_0(t, x)$$

then it is obvious (see Fig. 1c) that we can make $T_{\varepsilon}(x^*)$ quite long by choosing

$$\frac{1-\sqrt{\varepsilon}}{2} \equiv \frac{\beta x^{*n}}{1+\beta x^{*n}} \equiv \lim_{t \to \infty} u_0(t, x^*)$$
(53)

If we could further arrange that

$$u_0(t=0, x^*) \equiv \beta x^{*n} \leqslant \frac{1+\sqrt{\varepsilon}}{2}$$
(54)

then we would have solutons whose variance would always satisfy condition (47). Comparison of conditions (53) and (54) indicates that it is

294

necessary for ε to satisfy $(\sqrt{5}-2)^2 < \varepsilon \leq 1$ for this to be at all possible, or that $0.0057 < \varepsilon \leq 1$. Further, it will be more likely that this can be realized when $x^* = 1$.

The observation that when the mean value $\bar{\alpha}$ of the noise is in the neighborhood of *nr* there is a prolongation of the time T_{ε} over which (47) is satisfied [it may even be the case that (47) is satisfied for the entire trajectory when $\bar{\alpha} = nr$] highlights an interesting point. Namely, the presence of parametric noise can serve to probe for the existence of chaotic behavior in the solutions of equations like (1) when the conditions of Theorem 4 are satisfied. This conclusion is easy to understand once it is realized that the parametric noise on α , in the example we have presented using the initial function (17), is equivalent to probing the space Ξ_w of initial functions.

ACKNOWLEDGMENTS

This research was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) and by NATO.

REFERENCES

- 1. J. A. J. Metz and O. Diekmann, eds., *The Dynamics o Physiologically Structured Populations* (Springer-Verlag, New York, 1986).
- P. Brunovský, Notes on chaos in the cell population partial differential equation, Nonlinear Anal. 7:167-176 (1983).
- 3. P. Brunovský and J. Komorník, Ergodicity and exactness of the shift on $C[0, \infty]$ and the semiflow of a first order partial differential equation, J. Math. Anal. Appl. 104:235-245 (1984).
- A. Lasota, Stable and chaotic solutions of a first order partial differential equation, Nonlinear Anal. 5:1181-1193 (1981).
- K. Łoskot, Turbulent solutions of a first order partial differential equation, J. Differential Equations 58:1-14 (1985).
- 6. R. Rudnicki, Invariant measures for the flow of a first order partial differential equation, *Ergodic Theory Dynamic Syst.* **5**:437-443 (1985).
- 7. R. Rudnicki, An abstract Wiener measure invariant under a partial differential equaton, Bull. Pol. Acad. Sci. (Math.) 35:289-295 (1987).
- R. Rudnicki, Strong ergodic properties of a first order partial differential equation, J. Math. Anal. Appl. 132:14-26 (1988).
- 9. A. Lasota, K. Łoskot, and M. C. Mackey, Stability properties of proliferatively coupled cell replication models, *Acta Biotheor*. **39**:1-14 (1991).
- A. Lasota, M. C. Mackey, and M. Wazewska-Czyzewksa, Minimizing therapeutically induced anemia, J. Math. Biol. 19:43–62 (1981).
- M. C. Mackey and P. Dörmer, Continuous maturation of proliferating erythroid precursors, *Cell Tiss. Kinet.* 15:381–392 (1982).
- 12. A. Lasota and M. C. Mackey, *Probabilistic Properties of Deterministic Systems* (Cambridge University Press, Cambridge, 1985).