Fields Institute Communications
Volume **00**, 0000

Statistical Stability of Strongly Perturbed Dynamical Systems

Andrzej Lasota
Institute of Mathematics
Silesian University
ul. Bankowa 14
40–007 Katowice, Poland

Michael C. Mackey
Departments of Physiology, Physics, and Mathematics
Centre for Nonlinear Dynamics in Physiology and Medicine
McGill University
3655 Drummond
Montreal, Canada H3G 1Y6

Abstract. In this note we outline the study of the asymptotic behaviour of randomly perturbed dynamical systems from a statistical point of view, using four different techniques. The results are formulated in the language of Markov operator theory. Each technique is applied to a typical biological model. We also show an extension of the last technique – the Foguel alternative – to continuous time systems and its application to the logistic equation with parametric noise.

1 Introduction

It has been known for many years that randomly perturbed dynamical systems can be effectively studied by the use of Markov operators. Recently discovered methods in the theory of Markov operators facilitate this study. The purpose of this lecture is to present a few of these techniques which, in our opinion, are of great potential value, and to illustrate their use with applications to different biological models.

In Section 2 we start with a description of discrete time stochastically perturbed systems, and derive the corresponding transition operators. Then in Section 3 we review some basic facts from the theory of Markov operators, and outline four techniques which allow one to determine the asymptotic behaviour of perturbed systems from a statistical point of view. Sections 4 and 5 are devoted to the lower bound function technique and its application to mathematical models of the cell

1991 *Mathematics Subject Classification.* Primary 60J05, 92D25; Secondary 45D05, 47B38.

This research was partially supported by grants from the State Committee for Scientific Research (Poland), the Natural Sciences and Research Council (NSERC, Canada), and Le Fonds pour la Formation de Chercheurs et l'Aide à la Recherche (FCAR, Québec).

cycle. In Section 6 we present the asymptotic decomposition theorem, and show how it can be used to describe dynamical systems with additive and multiplicative perturbations. In Section 7 we study integral operators having a positive invariant density and we show an application to the Tyson–Hannsgen model of the cell cycle. Finally in Sections 8 and 9 we present a new version of the Foguel alternative and its application to the parametrically perturbed logistic equation. We also formulate an open problem concerning the existence of a subinvariant function for integral operators of Volterra type with advanced argument.

Most of the results discussed here are relatively new (e.g. Baron & Lasota [1993], Lasota & Mackey [1994], Malczak [1992]) or were especially prepared for this note. In particular we present new proofs of the asymptotic stability for the Tyson & Hannsgen and Tyrcha models of the cell cycle and also show new applications of the Foguel alternative.

2 Perturbed Dynamical Systems

We consider a stochastically perturbed discrete time dynamical system of the form

$$x_{n+1} = T(x_n, \xi_n), \quad n = 0, 1, \dots , \tag{2.1}$$

where x_n is the state variable of the system at time $t = n$ and the ξ_n are independent random variables which represent the perturbations. Throughout we make the following assumptions:

1. The transformation $T : X \times W \to X$ is defined on a set $X \times W$ where $X \subset I\!R^d$ is a closed set and $W \subset I\!R^k$ is Borel measurable. For every fixed $w \in W$ the function $T(x, w)$ is continuous in x and for every fixed $x \in X$ it is Borel measurable in w.
2. The random variables $\xi_0, \xi_1, \dots$ with values in W are independent and have the same distribution,
$$\nu(B) = \text{prob}\,(\xi_n \in B), \quad B \subset W, \quad B \text{ Borelian.}$$
3. The initial vector x_0 with values in X is independent of $\{\xi_n\}$.

Our goal is to study the statistical properties of the trajectories $\{x_n\}$. Thus we define the corresponding sequence of distributions

$$\mu_n(A) = \text{prob}\,(x_n \in A), \quad A \subset X, \quad A \text{ Borelian,}$$

and look for a recurrence relation that will give μ_{n+1} in terms of μ_n.

Let h be a real valued bounded Borel measurable function defined on X. Then the mathematical expectation of $h(x_{n+1})$ is given by the formula

$$E(h(x_{n+1})) = \int_X h(x)\mu_{n+1}(dx). \tag{2.2}$$

On the other hand, using (2.1), we have $h(x_{n+1}) = h(T(x_n, \xi_n))$ and consequently

$$E(h(x_{n+1})) = \int_X \int_W h(T(x, w))\mu_n(dx)\nu(dw). \tag{2.3}$$

From equations (2.2), (2.3), in the special case where $h = 1_A$ is the indicator function of a set A, we obtain

$$\mu_{n+1}(A) = \int_X \int_W 1_A(\,T(x, w)\,)\mu_n(dx)\nu(dw). \tag{2.4}$$

This is the desired recurrence condition. If the μ_n are absolutely continuous measures with densities $f_n(x) = d\mu_n/dx$ then equation (2.4) also allows us to calculate

f_{n+1} from f_n. In this case we write $f_{n+1} = Pf_n$ and we call P the *transition operator* corresponding to the dynamical system (2.1). We illustrate this situation by two important examples.

Example 2.1 Additive Perturbations. Assume that $X = W = I\!R^d$ and that $T(x,w)$ is linear in w, so $T(x,w) = S(x) + w$ with a continuous $S : I\!R^d \to I\!R^d$. In this case (2.1) reduces to

$$x_{n+1} = S(x_n) + \xi_n, \qquad n = 0, 1, \dots , \tag{2.5}$$

and (2.4) takes the form

$$\mu_{n+1}(A) = \int_{I\!R^d} \int_{I\!R^d} 1_A(S(x) + w)\mu_n(dx)\nu(dw).$$

If in addition we assume that the measure ν is absolutely continuous with a density g, then

$$\mu_{n+1}(A) = \int_{I\!R^d} \left\{ \int_{I\!R^d} 1_A(S(x) + w)g(w)dw \right\} \mu_n(dx).$$

Substituting $x = u,\ S(x) + w = y$ and changing the order of integration we obtain

$$\mu_{n+1}(A) = \int_A \left\{ \int_{I\!R^d} g(y - S(u))\mu_n(du) \right\} dy.$$

The function inside the braces is integrable with respect to y and consequently μ_{n+1} is an absolutely continuous measure. Therefore the densities $f_n = d\mu_n/dx$ exist for $n \geq 1$ and satisfy the recurrence relation $f_{n+1} = Pf_n$ with the transition operator

$$Pf(x) = \int_{I\!R^d} g(x - S(u))f(u)du. \tag{2.6}$$

Example 2.2 Multiplicative Perturbations. Assume that $X = W = [0, \infty)$ and that $T(x,w) = wS(x)$ with a continuous $S : [0, \infty) \to (0, \infty)$. Then

$$x_{n+1} = \xi_n S(x_n), \qquad n = 0, 1, \dots \tag{2.7}$$

and

$$\mu_{n+1}(A) = \int_0^\infty \int_0^\infty 1_A(wS(x))\mu_n(dx)\nu(dw). \tag{2.8}$$

Again assuming that ν is absolutely continuous with $d\nu/dx = g(x)$ and substituting $x = u,\, wS(x) = y$ we obtain

$$\mu_{n+1}(A) = \int_A \left\{ \int_0^\infty g\left(\frac{y}{S(u)} \right) \frac{\mu_n(du)}{S(u)} \right\} dy.$$

Thus for $n \geq 1$ the μ_n are absolutely continuous and the densities $f_n = d\mu_n/dx$ satisfy the relation $f_{n+1} = Pf_n$ where

$$Pf(x) = \int_0^\infty g\left(\frac{x}{S(u)} \right) f(u) \frac{du}{S(u)}. \tag{2.9}$$

In these two special cases the transition operator P was derived under the mild assumption that the distribution ν of perturbations is absolutely continuous. An analogous calculation can be carried out for the general form of $T(x,y)$. However, in this general situation the derivation of P is less transparent and requires some additional assumptions concerning the derivatives $\partial T/\partial w$. In the next section we will discuss the transition operators from a more abstract point of view.

3 Markov Operators

Let $(X, \mathcal{A}, \mu)$ be a σ–finite measure space. By D we denote the set of all normalized densities, i.e.

$$D = \{f \in L^1 : \ f \geq 0, \ \|f\| = 1\},$$

where $\|\cdot\|$ stands for the norm in $L^1 = L^1(X, \mathcal{A}, \mu)$. A linear mapping $P : L^1 \to L^1$ is called a *Markov operator* if $P(D) \subset D$.

An important class of Markov operators is given by stochastic kernels. We say that a measurable function $k : X \times X \to I\!R$ is a stochastic kernel if

$$k(x,z) \geq 0 \quad \text{and} \quad \int_X k(u,z)\mu(du) = 1, \quad x,z \in X. \tag{3.1}$$

Having k, we define the corresponding *integral Markov* operator by the formula

$$Pf(x) = \int_X k(x,u)f(u)\mu(du). \tag{3.2}$$

Conditions (3.1) imply that P given by (3.2) is in fact a Markov operator.

The transition operators (2.6) and (2.9) are typical examples of integral Markov operators. Conversely, it is interesting that every integral Markov operator is a transition operator of some stochastically perturbed dynamical system of the form (2.1). We may easily demonstrate this fact for operators defined on $L^1(I\!R)$. Thus assume that an integral Markov operator

$$Pf(x) = \int_{-\infty}^{+\infty} k(x,u)f(u)du, \tag{3.3}$$

is given. Assume moreover that $g \in D(I\!R)$ is an arbitrary positive ($g(x) > 0$ a.e.) density. Having k and g we define the function $T : I\!R \times I\!R \to I\!R$ as follows. For every fixed $(x,w) \in I\!R^2$ the value $T(x,w)$ is given as the smallest solution of the equation.

$$\int_{-\infty}^{T(x,w)} f(u,x)du = \int_{-\infty}^{w} g(u)du. \tag{3.4}$$

Since the integral on the right hand side of (3.4) has values in the open interval $(0,1)$ and k is a stochastic kernel the solution $T(x,w)$ always exists. An elementary calculation shows that the dynamical system $x_{n+1} = T(x_n, \xi_n)$, in which the ξ_n are independent random variables having the same density distribution function g, has a transition operator of the form (3.3). Formula (3.4) was proposed by K. Łoskot.

From the above considerations it follows that in many cases the study of the asymptotic behaviour of the perturbed dynamical system (2.1) can be replaced by the examination of the iterates $\{P^n\}$ of its transition operator P.

We introduce two simple definitions which describe the typical behaviour of $\{P^n\}$, assuming that a σ–finite measure space $(X, \mathcal{A}, \mu)$ is given.

A Markov operator $P : L^1 \to L^1$ is called *asymptotically stable* if there exists a density f_* such that $Pf_* = f_*$ and

$$\lim_{n\to\infty} \|P^n f - f_*\| = 0 \quad \text{for} \quad f \in D. \tag{3.5}$$

A density f_* satisfying $Pf_* = f_*$ is called stationary. Evidently (3.5) implies that for an asymptotically stable operator there exists exactly one stationary density.

Let a Markov operator $P : L^1 \to L^1$ and a subfamily of measurable subsets $\mathcal{A}_* \subset \mathcal{A}$ be given. We say that P is *sweeping* with respect to $\mathcal{A}_*$ (or, simply, sweeping) if

$$\lim_{n\to\infty} \int_A P^n f(x)\mu(dx) = 0 \quad \text{for} \quad A \in \mathcal{A}_*, \quad f \in D. \tag{3.6}$$

We say that the family $\mathcal{A}_*$ is *regular* if there exists a sequence $A_n \in \mathcal{A}_*$ such that $X = \bigcup_n A_n$. Evidently an operator which is sweeping with respect a regular family $\mathcal{A}_*$ cannot be asymptotically stable.

In the following sections we will show four effective criteria for the determination of asymptotic stability and sweeping. Namely we will discuss:

1. the lower bound function theorem,
2. asymptotic decomposition of constrictive operators,
3. integral operators satisfying a transitivity property,
4. the Foguel alternative.

Each criterion will be illustrated by an application to a dynamical system. In particular we will examine some mathematical models of the cell cycle and the logistic growth equation with parametric noise.

4 Lower Bound Function

Let $(X, \mathcal{A}, \mu)$ be a σ–finite measure space and $P : L^1 \to L^1$ a Markov operator. We say that a function $h \in L^1$ is a *lower bound function* if for every $f \in D$ there is a sequence $\varepsilon_n(f) \in L^1$ such that

$$P^n f \geq h - \varepsilon_n(f) \quad \text{and} \quad \|\varepsilon_n(f)\| \to 0. \tag{4.1}$$

A lower bound function h is nontrivial if $h \geq 0$ and $\|h\| > 0$.

At first glance conditions (4.1) look much weaker than condition (3.5) appearing in the definition of the asymptotic stability. We have, however, the following theorem from Lasota & Yorke [1982].

Theorem 4.1 *A Markov operator P is asymptotically stable if and only if it has a nontrivial lower bound function.*

An efficient condition to prove the asymptotic stability of integral Markov operators can be formulated by a use of a Liapunov function. Let $G \subset I\!R^d$ be an unbounded Borel measurable set. A continuous function $V : G \to I\!R$ is called a Liapunov function if

$$V(x) \geq 0 \quad \text{for} \quad x \in G \quad \text{and} \quad \lim_{|x|\to\infty} V(x) = \infty.$$

Consider on $L^1(G)$ an integral Markov operator

$$Pf(x) = \int_G k(x,y) f(y)dy. \tag{4.2}$$

From Theorem 4.1 it is easy to derive the following corollary which is a slight generalization of a result of Tyrcha [1988].

Assume that there exists a Liapunov function V and constants $\delta \geq 0$, $\gamma < 1$ such that

$$\int_G V(x)Pf(x)dx \leq \delta + \gamma \int_G V(x)f(x)dx \quad \text{for} \quad f \in D. \tag{4.3}$$

Assume moreover that

$$\int_G \inf_{u\in C} k(x,u)dx > 0 \tag{4.4}$$

for every compact set $C \subset G$. Then the operator P defined by (4.2) is asymptotically stable.

5 A Cell Cycle Model

As an example of the applicability of the lower bound function technique we consider a model of cell cycle proposed by Tyrcha [1988] which generalizes a model of Lasota & Mackey [1984] and the tandem model of Tyson & Hannsgen [1986].

In the Tyrcha model it is assumed that the cell cycle consists of two phases A and B. Phase A begins at birth and lasts until the occurrence of a critical event which is necessary for mitosis. Then the cell enters phase B. The end of phase B coincides with cell division. The duration t_B of phase B is constant while the length t_A of phase A is random. More precisely the probability that the critical moment occurs in the interval $[t, t+\Delta t]$ is

$$\text{prob}\,(t \le t_A \le t + \Delta t \mid t_A \ge t) = \varphi(x(t))\Delta t + o(\Delta y), \tag{5.1}$$

where $x(t)$ is the size (or amount of mitogen) of the cell at time t and φ is a given nonnegative function. Further it is assumed that the cell size grows according to the equation

$$\frac{dx}{dt} = g(x), \qquad x(0) = r, \tag{5.2}$$

where $g(x)$ for $x > 0$ and $g(0) = 0$. Denote by x_n the initial size of cell in the n–th generation. Evidently x_n can be considered as a random variable. Using the above assumptions it can be shown (see Lasota *et al.* [1992]) that

$$x_{n+1} = \lambda^{-1}\{Q^{-1}[\,Q(x_n) + \xi_n\,]\}, \tag{5.3}$$

where

$$Q(x) = \int_0^x \tfrac{\varphi(y)}{g(y)}dy, \qquad \lambda(x) = \pi(-t_B, 2x)$$

and $\pi(t,x)$ is the solution of equation (5.2). The random variables ξ_n are independent and have the common density distribution function $g(x) = \mathrm{e}^{-x}$. An elementary calculation shows that the transition operator for the dynamical system (5.3) has the form

$$Pf(x) = -\int_0^{\lambda(x)} \Big\{\tfrac{\partial}{\partial x}\exp[Q(y) - Q(\lambda(x))]\Big\} f(y)dy. \tag{5.4}$$

The asymptotic properties of operator (5.4) can be studied under the quite general assumptions that Q and λ are absolutely continuous, nondecreasing and

$$\lim_{x\to\infty} Q(x) = \lim_{x\to\infty} \lambda(x) = \infty, \qquad \lambda(0) = 0. \tag{5.5}$$

These condition imply by a straightforward calculation that P is an integral Markov operator on $L^1([0,\infty))$. The asymptotic behaviour of P is described by the following.

Theorem 5.1 *If*

$$\liminf_{x\to\infty}[\,Q(\lambda(x)) - Q(x)\,] > 1, \tag{5.6}$$

then P is asymptotically stable, and if

$$\limsup_{x\to\infty}[\,Q(\lambda(x)) - Q(x)\,] < 1, \tag{5.7}$$

then P is sweeping with respect to compact subsets of $[0,\infty)$.

Proof (outline). First assume (5.6) setting $V(x) = \exp(\alpha Q(\lambda(x)))$, $0 < \alpha < 1$, so using (5.4) it is easy to verify that

$$\int_0^\infty V(x)Pf(x)dx = \tfrac{1}{1-\alpha}\int_0^\infty f(x)e^{\alpha Q(x)}dx. \tag{5.8}$$

According to (5.6), there exists an $x_0 > 0$ and $\varrho > 1$ such that $Q(x) \le Q(\lambda(x)) - \varrho$ for $x \ge x_0$. Using this and (5.8) we obtain

$$\int_0^\infty V(x)Pf(x)dx \le \tfrac{1}{1-\alpha}\int_0^{x_0} f(x)e^{\alpha Q(x)}dx + \tfrac{e^{-\varrho\alpha}}{1-\alpha}\int_{x_0}^\infty V(x)f(x)dx$$

or

$$\int_0^\infty V(x)Pf(x)dx \le \delta(\alpha) + \gamma(\alpha)\int_0^\infty V(x)f(x)dx,$$

where $\delta = e^{\alpha Q(x_0)}(1-\alpha)^{-1}$ and $\gamma(\alpha) = e^{-\varrho\alpha}(1-\alpha)^{-1}$. The inequality $\varrho > 1$ implies that $\gamma(\alpha) < 1$ for some $\alpha \in (0,1)$ and consequently condition (4.3) of Corollary 4.1 is satisfied. The verification of (4.4) is elementary due to the specific (exponential) form of the kernel in (5.4).

Now assume (5.7) and define $V(x) = w(\,Q(\lambda(x))\,)$ where

$$w(x) = \begin{cases} e^{-\alpha x_0} & \text{for } x \le x_0\ , \\ e^{-\alpha x} & \text{for } x > x_0\ . \end{cases}$$

Choosing x_0 sufficiently large and $\alpha > 0$ sufficiently small it can be shown that

$$\int_0^\infty V(x)Pf(x)dx \le \gamma\int_0^\infty V(x)f(x)dx, \quad \text{for} \quad f \in D, \tag{5.9}$$

where $\gamma < 1$ is a constant. From (5.9) follows

$$\lim_{n\to\infty}\int_0^\infty V(x)P^nf(x)dx = 0$$

which implies sweeping. □

The detailed proof is given in Gacki & Lasota [1990]. The proof presented here is much shorter due to another choice of the Liapunov function $V(x)$.

6 Asymptotic Decomposition Theorem

In order to apply the lower bound function technique it is necessary to evaluate the sequence $\{P^nf\}$ from below. The asymptotic decomposition theorem also describes the behaviour of $\{P^nf\}$ in the case when the sequence $\{P^nf\}$ has an integrable upper bound.

Let $(X, \mathcal{A}, \mu)$ be a σ–finite measure space. A Markov operator $P : L^1 \to L^1$ is called *constrictive* if there exists constant $\kappa < 1$, $\delta > 0$ and a set $C \in \mathcal{A}$ with the following property: For every $f \in D$ there is an integer $n_0(f)$ such that

$$\int_{B\cup(X\setminus C)} P^nf(x)\mu(dx) \le \kappa \quad \text{for} \quad n \ge n_0(f), \quad \mu(B) \le \delta, \quad B \subset C. \tag{6.1}$$

The constrictivness rules out the possibility that for large n the densities P^nf are either concentrated on a set of very small measure or dispersed throughout the entire space. In particular P is constrictive if there exists an integrable function $h \ge 0$ such that

$$P^nf \le h + \varepsilon_n(f) \quad \text{and} \quad \lim_{n\to\infty}\|\varepsilon_n(f)\| = 0.$$

The asymptotic behaviour of constrictive operators is described by the following theorem due to Komornik & Lasota [1987].

Theorem 6.1 *The iterates of a constrictive operator P can be written in the form*

$$P^n f = \sum_{i=1}^{r} \lambda_i(f) g_{\alpha^n(i)} + Q_n f, \quad \text{for } f \in L^1, \tag{6.2}$$

where:

1. $g_1, \dots, g_r$ *are densities with disjoint supports;*
2. $\lambda_1, \dots \lambda_r$ *are linear functionals on* L^1*;*
3. α *is a permutation of numbers* $1, \dots, r$ *such that* $Pg_i = g_{\alpha(i)}$ *and* α^n *denotes the* n^{th} *iterate of* α*;*
4. Q_n *is a sequence of operators such that* $\lim_{n\to\infty} \|Q_n f\| = 0$ *for* $f \in L^1$.

The terms under the summation in (6.2) are just permuted with each application of P and since r is finite this sum is periodic with a period smaller than or equal to $r!$. Thus for every $f \in L^1$ the sequence $\{P^n f\}$ is asymptotically periodic. From Theorem 6.1 it is easy to derive a simple criterion for asymptotic stability.

Let P be a constrictive Markov operator. Assume there is a set $A \in \mathcal{A}$ of positive measure with the following property: For every $f \in D$ there exists an integer $n_0(f)$ such that

$$P^n f(x) > 0 \quad \text{for } x \in A \text{ a.e. and } n \geq n_0. \tag{6.3}$$

Then P is asymptotically stable.

Theorem 6.1 and Corollary 6.1 can be easily applied to dynamical systems with additive and multiplicative perturbations. We show this application in the following two examples.

Example 6.2 Again consider the dynamical system (2.5) and the corresponding transition operator (2.6). Assume that there is a number $M > 0$ such that for every initial vector x_0 the sequence $\{x_n\}$ satisfies

$$\limsup_{n\to\infty} E(|x_n|) < M. \tag{6.4}$$

Then by the Chebyshev inequality

$$\int_{|x|\geq 2M} P^n f(x)dx \leq \tfrac{E(|x_n|)}{2M} \leq \tfrac{1}{2}$$

for $f \in D$ and n sufficiently large, say $n \geq n_0(f)$. Moreover for $f \in D$ we have

$$\begin{aligned} \int_B P^n f(x)dx &= \int_B \left\{ \int_{IR^d} g(x - S(u)) P^{n-1} f(u) du \right\} dx \\ &\leq \sup_{z\in \mathbb{R}^d} \int_{B+z} g(x)dx. \end{aligned}$$

Since g is Lebesgue integrable, there exists a $\delta > 0$ such that the last integral is smaller than $\varepsilon = 1/4$ whenever $\mu(B) \leq \delta$. Setting $C = \{x : |x| \leq 2M\}$ we have

$$\int_{B\cup(\mathbb{R}^d\setminus C)} P^n f(x)dx \leq \int_B P^n f(x)dx + \int_{|x|\geq 2M} P^n f(x)dx \leq \tfrac{3}{4}$$

for $f \in D$ and $n \geq n_0(f)$ which implies constrictivness. Thus, using Theorem 6.1 we obtain the following conclusion: Every dynamical system with additive perturbations is either asymptotically unbounded ((6.4) is not satisfied with any M

independent of x_0) or the sequence of densities $\{P^n f\}$ is asymptotically periodic. If (6.4) is satisfied and in addition $g(x) > 0$ for $x \in I\!R^d$, then condition (6.3) is also fullfilled and $\{P^n f\}$ converges to a unique stationary density.

Example 6.3 Now consider the dynamical system (2.7) with the transition operator (2.9). Assume that the transformation S is linearly bounded, i.e.

$$0 < S(x) \le \alpha x + \beta \quad \text{for} \quad x \ge 0, \tag{6.5}$$

and that the perturbations ξ_n have a common density distribution function g with a finite first moment

$$m = \int_0^\infty x g(x)dx < \infty. \tag{6.6}$$

Horbacz [1989] has shown that for $\alpha m < 1$ the operator P given by (2.9) is constrictive. A simplified version of her proof goes as follows. Setting $V(x) = x$ it is easy to verify that

$$\begin{aligned}\int_0^\infty V(x)Pf(x)dx &= m\int_0^\infty f(x)S(x)dx \\ &\le \alpha m\int_0^\infty V(x)f(x)dx + \beta m,\end{aligned}$$

which shows that condition (4.3) of Corollary 4.1 is satisfied. This, by the Chebyshev inequality, implies

$$\int_0^c P^n f(x)dx \ge \tfrac{3}{4} \quad \text{for} \quad n \ge n_0(f),$$

where c is a sufficiently large number. Since g is integrable there must be a $\delta_1 > 0$ such that

$$\int_A g(x)dx \le \tfrac{1}{4} \quad \text{for} \quad \mu(A) \le \delta_1.$$

Define $\delta = \delta_1 \min\limits_{0\le u\le c} S(u)$. Then for $\mu(B) \le \delta$ and $0 \le u \le c$ we have $\mu(B/S(u)) \le \delta_1$. Consequently

$$\begin{aligned}\int_B P^n f(x)dx &= \int_0^\infty P^{n-1}f(u)\Big\{\int_B g\Big(\tfrac{x}{S(u)}\Big)\tfrac{dx}{S(u)}\Big\}du \\ &\le \int_c^\infty P^{n-1}f(u)du + \int_0^c P^{n-1}f(u)\Big\{\int_B g\Big(\tfrac{x}{S(u)}\Big)\tfrac{dx}{S(u)}\Big\}du \\ &\le \tfrac{1}{4} + \tfrac{1}{4}\int_0^c P^{n-1}f(u)du \;\le\; \tfrac{1}{2} \qquad \text{for} \quad n \ge n_0(f)+1.\end{aligned}$$

Setting $X = [0,\infty),\ C = [0,c]$ we have $X \setminus C = [c,\infty)$ and

$$\int_{B\cup(X\setminus C)} P^n f(x)dx \le \int_B P^n f(x)dx + \int_0^\infty P^n f(x)dx \le \tfrac{1}{2} + \tfrac{1}{4}$$

which again shows that P is constrictive. If in addition $g(x) > 0$ for $x > 0$ then $Pf(x) > 0$ for $x > 0$ and condition (6.3) is automatically satisfied. In this case P is asymptotically stable.

In the above argument, the conditions $S(x) > 0$ for $x \ge 0$ and $g(x) > 0$ for $x > 0$ play an important role. A more sophisticated argument given by Horbacz [1989] shows that P remains asymptotically stable if

$$S(0) = 0, \quad S(x) > 0 \;\text{ for }\; x > 0, \quad g(x) > 0 \;\text{ for }\; x \;\text{ sufficiently large.}$$

However in this case it is assumed not only that $\alpha m < 1$ but also that

$$\int_0^\infty \frac{g(x)}{(\gamma x)^\lambda} < 1, \qquad \gamma = S'(0) \tag{6.7}$$

for some $\lambda > 0$. The Horbacz result can be applied to the "bottleneck" model of annual plants with "seedbank" studied by Watkinson [1980] and Ellner [1984]. The dynamical system describing this model can be written in the form

$$x_{n+1} = \frac{\xi_n x_n}{(1+(k+p)x_n)^\alpha (1+px_n)^{1-\alpha}},$$

where $\alpha,\ k,\ p$ are positive constants and x_n is the size of the population in the n^{th} generation. According to Horbacz the bottleneck model is asymptotically stable if the density $g(x)$ of perturbation ξ_n is positive for large x and

$$\int_0^\infty \frac{g(x)}{x^\lambda} dx < 1$$

for some $\lambda > 0$.

7 Transitive Integral Operators

In this section we discuss Markov operators defined by the integral equation (3.2), i.e.

$$Pf(x) = \int_X k(x,u) f(u) \mu(du), \tag{7.1}$$

where, as before, $(X, \mathcal{A}, \mu)$ is a $\sigma-$ finite measure space and $k : X \times X \to I\!R$ is a stochastic kernel. Integral Markov operators have some specific properties which simplify the conditions for the convergence of iterates. Namely, the existence of an invariant density and a simple transition property imply asymptotic stability. To formulate this criterion precisely, recall that in the theory of Markov operators the support of an $f \in L^1$ is defined by

$$\operatorname{supp} f = \{x \in X : \ f(x) \neq 0\}.$$

We say that an operator $P : L^1 \to L^1$ *overlaps supports* if for every $f, g \in D$ there is an $n_0(f,g)$ such that

$$\mu(\operatorname{supp} P^{n_0} f \cap \operatorname{supp} P^{n_0} g) > 0. \tag{7.2}$$

Baron & Lasota [1993] have proved the following

Theorem 7.1 *An integral Markov operator which overlaps supports and has a positive stationary density* ($f_*(x) > 0$ *a.e.*) *is asymptotically stable.*

Using Theorem 7.1 it is possible to find a sharp sufficient condition for the asymptotic stability of the operator

$$Pf(x) = \int_0^{\lambda(x)} \left\{ -\frac{\partial}{\partial x} H(\, Q(\lambda(x)) - Q(u)\,) \right\} f(u) du \tag{7.3}$$

which appears in the general model of irregular biological events proposed by Lasota *et al.* [1992]. Formula (7.3) represents the transition operator for dynamical system of the form (5.3) in which the perturbations ξ_n have the common survival function

$$\operatorname{prob}(\xi_n > x) = H(x).$$

This application is, however, quite complicated and we are not going to present it here. For the sake of simplicity we show how Theorem 7.1 can be applied to the

Tyson & Hannsgen model of the cell cycle. In this model the transition operator $P : L^1([\sigma,\infty)) \to L^1([\sigma,\infty))$ has the form

$$Pf(x) = \int_{\sigma}^{x/\sigma} K(x,u)f(u)du, \tag{7.4}$$

where

$$K(x,u) = \begin{cases} (\alpha/\sigma)(x/\sigma)^{-1-\alpha} & \text{for } \sigma \le u \le 1, \\ (\alpha/\sigma)(x/\sigma)^{-1-\alpha}u^{\alpha} & \text{for } 1 < \sigma \le x/\sigma. \end{cases} \tag{7.5}$$

and $\alpha > 0$, $0 < \sigma < 1$ are constants. The operator (7.4) evidently overlaps supports, since for every $f \in D$ the values $Pf(x)$ are positive if x is sufficiently large. Further an immediate calculation shows that the function

$$f_*(x) = \frac{c}{x^{\beta+1}}\ , \qquad x \ge \sigma \tag{7.6}$$

is invariant with respect to P if β is a solution to the transcendental equation

$$w(\beta) := \sigma^{\beta} + \beta/\alpha = 1. \tag{7.7}$$

Such a solution $\beta > 0$ exists if $w'(0) < 1$ or

$$\alpha > -\frac{1}{\ln\sigma}. \tag{7.8}$$

In this case (7.6) with a properly chosen c is a positive invariant density on $[\sigma,\infty)$ and according to Theorem 7.1 the operator P defined by (7.4), (7.5) is asymptotically stable.

The fact that condition (7.8) implies asymptotic stability of P was already predicted by Tyson & Hannsgen [1986]. They also found the stationary density (7.6) and proved the asymptotic stability under more restrictive condition $\alpha > 1/(1-\sigma)$. The first proof that (7.8) actually implies asymptotic stability was given by Tyrcha [1988]. Another proof follows from the result of Gacki & Lasota [1990]. This short history of stability conditions for operator (7.4), (7.5) shows the utility of Theorem 7.1. Once a positive stationary density is found the proof of stability is easy. It remains only to verify the "overlapping support" property.

In the next section we present a theorem which can be used not only to prove asymptotic stability, but also sweeping.

8 The Foguel Alternative

Let a σ–finite measure space and a regular family $\mathcal{A}_* \subset \mathcal{A}$ be given. In order to formulate the main result of this section – the Foguel alternative – we need to introduce a few notions.

A measurable function $f : X \to I\!R$ is called *locally* integrable if

$$\int_A f(x)\mu(dx) < \infty \qquad \text{for } A \in \mathcal{A}_*.$$

A Markov operator P is called *expanding* if

$$\lim_{n\to\infty} \mu(A \setminus \operatorname{supp} P^n f) = 0 \qquad \text{for} \qquad f \in D,\ \ \mu(A) < \infty. \tag{8.1}$$

Finally, a measurable nonnegative function $h : X \to I\!R$ is called *subinvariant* with respect to an integral operator P given by (7.1) if

$$Ph(x) := \int_X k(x,u)h(u)\mu(du) \le h(x) \qquad \text{a.e.}$$

Using the result of Komorowski & Tyrcha [1989] and Malczak [1992] the following version of the Foguel alternative (Foguel [1966], Lin [1971]) can be stated.

Theorem 8.1 *Assume that P is an expanding integral operator and that there is a locally integrable positive subinvariant function h ($h > 0, Ph \leq h$ a.e.). Then either P is asymptotically stable or P is sweeping.*

A simple example of an operator P for which all the assumption of Theorem 8.1 are satisfied is given by the Tyson & Hannsgen equations (7.4), (7.5). In this case it is natural to assume that $\mathcal{A}_*$ consists of all compact subsets of $[\sigma, \infty)$. Since for every positive σ and α equation (7.7) has a solution $\beta = 0$, we may choose $h(x) = 1/x$ as an invariant locally integrable function. Finally condition (8.1) follows from the fact that $\sigma < 1$ and K given by (7.1) is positive.

The arguments used in the above example can be extended to a large family of Markov operators of the form

$$Pf(x) = \int_a^{\lambda(x)} K(x,u) f(u) du$$

in which $K(x,u) > 0$ for $a < u < \lambda(x)$, $x > a$ and $\lambda(x) > x$ for $x > a$ ($a \geq 0$). The only difficulty lies in the proof of the existence of a positive locally integrable subinvariant function. Thus, it is an important and open problem to characterize the class of kernels K and bounds λ for which such a function exists.

9 Foguel Alternative for Continuous Time Semigroups

The Foguel alternative may be easily extended to continuous time systems and applied to differential equations with stochastic perturbations. We are going to show such applications using the formalism of stochastic semigroups. As before we assume that $(X, \mathcal{A}, \mu)$ and a regular $\mathcal{A}_*$ are given.

A family $\{P_t\}_{t \geq 0}$ of Markov operators is called a (continuous) *stochastic semigroup* if the following conditions are satisfied.

1^o $P_0 f = f$ for $f \in L^1$;

2^o $P_{t+s} f = P_t(P_s f)$ for $t, s \geq 0$, $f \in L^1$;

3^o $\lim_{t \to 0} \|P_t f - f\| = 0$ for $f \in L^1$.

A stochastic semigroup is called *asymptotically stable* if there exists an $f_* \in D$ such that $P_t f_* = f_*$ (stationary density) and if

$$\lim_{t \to \infty} \|P_t f - f_*\| = 0 \quad \text{for} \quad f \in D .$$

A semigroup $\{P_t\}_{t \geq 0}$ is called *sweeping* if

$$\lim_{t \to \infty} \int_A P_t f(x) \mu(dx) = 0 \quad \text{for} \quad f \in D, \quad A \in \mathcal{A}_* .$$

Stability and sweeping of a stochastic semigroup $\{P_t\}_{t \geq 0}$ and a single operator P_t with a fixed t are closely related. It can be proved (Lasota & Mackey [1994]) that asymptotic stability of P_{t_0} with $t_0 > 0$ implies the asymptotic stability of $\{P_t\}_{t \geq 0}$ with the same stationary density f_*, and analogously that the sweeping of P_{t_0} implies the sweeping of $\{P_t\}_{t \geq 0}$. The inverse implications are obvious. Using this it is easy to derive from Theorem 8.1 the following.

Let $\{P_t\}_{t \geq 0}$ be a continuous stochastic semigroup. Assume that for some $t_0 > 0$ the operator P_{t_0} is expanding and given by a stochastic kernel. Assume moreover that there exists for P_{t_0} a positive locally integrable subinvariant function. Then either the semigroup $\{P_t\}_{t\geq 0}$ is asymptotically stable or $\{P_t\}_{t\geq 0}$ is sweeping.

As an example consider the logistic equation

$$\frac{dx}{dt} = x(a_1 - x), \qquad \text{with} \qquad a_1 = a + \sigma\xi_t, \tag{9.1}$$

where a, σ are positive constants and ξ_t is a normalized white noise. The density distribution function $u(t,x)$ of $x(t)$ satisfies the Fokker–Planck equation

$$\frac{\partial u}{\partial t} = \frac{\sigma^2}{2} \frac{\partial^2(x^2 u)}{\partial x^2} - \frac{\partial}{\partial x}[x(a-x)u] \tag{9.2}$$

and the corresponding stochastic semigroup is defined by

$$P_t f(x) = u(t,x), \qquad u(0,x) = f(x) \ .$$

In order to study the asymptotic behaviour of $\{P_t\}_{t\geq 0}$ it is not necessary to solve (9.2). It is enough to know that $u(t,x)$ is given by an integral formula

$$u(t,x) = \int_0^\infty \Gamma(t,x,y) f(y) dy$$

with a stochastic kernel (Green's function) Γ. We obtain the stationary density by solving the stationary equation

$$\frac{\sigma^2}{2} \frac{d^2(x^2 u(x))}{dx^2} - \frac{d}{dx}[x(a-x)u(x)] = 0$$

which gives

$$u(x) = f_*(x) = c x^\gamma \mathrm{e}^{-x/\sigma^2}, \tag{9.3}$$

where $\gamma = 2(a/\sigma^2) - 2$. This function is, for every γ, locally integrable with respect to the family

$$\mathcal{A}_* = \{ [\varepsilon, \infty) : \ \varepsilon > 0 \} \ . \tag{9.4}$$

If $\gamma > -1$ so $a > \frac{1}{2}\sigma^2$, the function (9.3) can be normalized and $\{P_t\}_{t\geq 0}$ has a stationary density. In this case $\{P_t\}_{t\geq 0}$ cannot be sweeping and by the Foguel alternative it is asymptotically stable. If the inverse inequality $a \leq \frac{1}{2}\sigma^2$ holds, then $\{P_t\}_{t\geq 0}$ has no stationary density and cannot be asymptotically stable. According to the Foguel alternative the semigroup $\{P_t\}_{t\geq 0}$ must be sweeping with respect to (9.4). This means that for large t, the density $u(t,x)$ is concentrated in a neighborhood of $x = 0$. A large parametric perturbation can kill the population.

References

Baron, K, & Lasota, A. [1993] *Asymptotic properties of Markov operators defined by Volterra type integrals.* Ann. Polon. Math. **58**, 161-175.

Ellner, S. [1984] *Asymptotic behaviour of some stochastic difference equation population models.* J. Math. Biology **19**, 169–200.

Foguel, S. R. [1966] *Limit theorems for Markov processes.* Trans. Amer. Math. Soc. **121**, 200–209.

Gacki, H. & Lasota, A. [1990] *Markov operators defined by Volterra type integrals with advanced argument.* Ann. Polon. Math. **51**, 155–166.

Horbacz, K. [1989] *Asymptotic stability of dynamical systems with multiplicative perturbations.* Ann. Polon. Math. **50**, 209–218.

Kormornik, J. & Lasota, A. [1987] *Asymptotic decomposition of Markov operators.* Bull. Polish Acad. Sci. Math. **35**, 321–327.

Komorowski, T. & Tyrcha, J. [1989] *Asymptotic properties of some Markov operators.* Bull. Polon. Acad. Sci. Math. **37**, 221–228.

Lasota, A. & Mackey, M.C. [1984] *Globally asymptotic properties of proliferating cell populations.* J. Math. Biology **19**, 43–62.

Lasota, A. & Mackey, M.C. [1994] *Chaos, Fractals and Noise: Stochastic Aspects of Dynamics.* (second edition), Springer Verlag, New York.

Lasota, A., Mackey, M.C., & Tyrcha, J. [1992] *The statistical dynamics of irregular biological events*, J. Math. Biol. **30**, 775–800.

Lasota, A. & Yorke, J.A. [1982] *Exact dynamical systems and the Frobenius–Perron operator.* Trans. Amer. Math. Soc. **273**, 375–384.

Lin, M. [1971] *Mixing for Markov operators.* Z. Wahrsheinlichkeitstheorie Verw. Gebiete **19**, 231–242.

Malczak, J. [1992] *An application of Markov operators in differential and integral equations.* Rend. Sem. Mat. Univ. Padova **87**, 281–297.

Tyrcha, J. [1988] *Asymptotic stability in a generalized probabilistic/deterministic model of the cell cycle.* J. Math. Biol. **26**, 465–475.

Tyson, J. J. & Hannsgen, K.B. [1986] *Cell growth and division: A deterministic/ probabilistic model of the cell cycle.* J. Math. Biol. **23**, 231–246.

Watkinson, A. R. [1980] *Density dependence in single–species population of plants.* J. Theor. Biol. **82**, 345–357.