

The Extinction of Slowly Evolving Dynamical Systems

A. Lasota¹ and Michael C. Mackey²

¹ Institute of Mathematics, Silesian University, ul. Bankowa 14, 40-007 Katowice, Poland

² Department of Physiology, McGill University, 3655 Drummond Street, Montreal, Quebec, Canada, H3G 1Y6

Abstract. The time evolution of slowly evolving discrete dynamical systems $x_{i+1} = T(r_i, x_i)$, defined on an interval $[0, L]$, where a parameter r_i changes slowly with respect to i is considered. For certain transformations T , once r_i reaches a critical value the system faces a non-zero probability of *extinction* because some $x_j \notin [0, L]$. Recent ergodic theory results of Ruelle, Pianigiani, and Lasota and Yorke are used to derive a simple expression for the probability of survival of these systems. The extinction process is illustrated with two examples. One is the quadratic map, $T(r, x) = rx(1 - x)$, and the second is a simple model for the growth of a cellular population. The survival statistics for chronic myelogenous leukemia patients are discussed in light of these extinction processes. Two other dynamical processes of biological importance, to which our results are applicable, are mentioned.

Key words: Ergodic theory – Extinction – Cell populations – Leukemia.

I. Introduction

The recent discovery that simple point to point transformations may display a spectrum of dynamic behaviours (including chaotic or stochastic-like behaviours) as a single parameter is varied has excited and intrigued a number of biologists [cf. May (1976) for a review]. Probably the simplest and most widely known example is the quadratic transformation

$$T(r, x) = rx(1 - x), \quad x \in [0, 1]. \quad (1)$$

There is a large literature characterizing the dynamics of this transformation for various values of the parameter r (Li and Yorke, 1976; Lorentz, 1964; May, 1976; Pianigiani, 1979a; Ruelle, 1977; Smale and Williams, 1976).

One of the most effective ways of describing the chaotic behaviour that transformations such as (1) may display is via the techniques of ergodic theory. If it is possible to prove the existence of a continuous stable invariant density with respect to any transformation T , then the statistical properties of the system may be immediately calculated. Thus, the chaos may be statistically characterized.

For the quadratic map (1), when $r = 4$, the density is known and thus all properties of the chaotic behaviour of this map may be computed. For many years this was the only regular convex function for which such results were available, no doubt contributing to the popularity of (1) in studies exploring the implications of "chaos" for biology. The recent elegant demonstration by Ruelle (1977) and Pianigiani (1979b) that the existence of a stable invariant density may be proved for a much larger class of convex regular functions than (1) opens a number of new and interesting possibilities for those interested in understanding biological phenomena.

Here, the time evolution of a dynamical system $x_{i+1} = T(r_i, x_i)$ defined on an interval $[0, L]$, where the parameter r_i changes at a small constant rate with time (i), is considered. For a certain class of transformations $T(r, x)$ which satisfy the Pianigiani-Ruelle conditions (cf. section II), once r_i reaches a critical value the system faces a non-zero probability of extinction because some $x_i \notin [0, L]$. For such a slowly evolving system, a simple equation giving the distribution of survival times is derived in section III. The nature of this extinction process is first illustrated in section IV by assuming that the quadratic transformation (1) is evolving slowly with respect to r , and comparing the analytic results with actual survival times from computer experiments. In a second example (section V) the extinction of a renewing cellular population, with a slowly increasing maximum cell production rate, is considered. As a concrete example of such a process, this mechanism is related to the survival of patients with chronic myelogenous leukemia.

Throughout this paper the evolution and extinction of systems is discussed in terms of distributions of points rather than speaking of distributions of measures. Although this sacrifices some degree of preciseness, it makes the arguments more directly applicable to biological problems. For an analogous treatment from a measure-theoretic point of view, see Lasota and Yorke (1979).

II. Mathematical Preliminaries

In this section, the concept of density and some simple properties of densities are introduced before stating a theorem which summarizes the recent results of Ruelle (1977) and Pianigiani (1979b) of importance for the problem of extinction in slowly evolving systems.

Let an interval $[0, L]$ be given. A *density* on $[0, L]$ is an arbitrary real valued function $f(x)$ satisfying $f(x) \geq 0$ for all $x \in [0, L]$ and

$$\int_0^L f(s) ds = 1.$$

The notion of density may be easily, but quite precisely understood in the following way. Suppose N points are distributed through the interval $[0, L]$ in some fashion. These points are said to be distributed according to a density $f(x)$ if any subinterval $[a, b]$ of the total interval $[0, L]$, which is sufficiently large with respect to the distance between points, the number of points in the interval $[a, b]$, $N_{[a,b]}$, is given by

$$N_{[a,b]} = N \int_a^b f(s) ds. \quad (2)$$

Suppose there is a function, or transformation, $T(x)$ which takes all of the points $x \in [0, L]$ and maps them into the same interval, $T(x) \in [0, L]$. Such a transformation is also written $T: [0, L] \rightarrow [0, L]$. The inverse image of an interval $[a, b]$ is written as $T^{-1}([a, b])$. The density, or distribution, $f(x)$, is said to be *invariant* with respect to T if the relation

$$\int_a^b f(s) ds = \int_{T^{-1}([a,b])} f(s) ds \tag{3}$$

holds for every interval $[a, b] \subset [0, L]$.

To understand the meaning of invariance, consider the following. Each of the original N points distributed in $[0, L]$ according to $f(x)$ are transformed by T to a new value, and the new set of points has a distribution $f_1(x)$. What is $f_1(x)$? Now

$$N_{[a,b]}^1 = N_{T^{-1}([a,b])} \tag{4}$$

where $N_{[a,b]}^1$ is the number of points in $[a, b]$ after one application of T . Thus from (2)

$$\int_a^b f_1(s) ds = \int_{T^{-1}([a,b])} f(s) ds. \tag{5}$$

Set $a = 0$, $b = x$ and differentiate (5) with respect to x to obtain

$$f_1(x) = \frac{d}{dx} \int_{T^{-1}([0,x])} f(s) ds \tag{6}$$

as the new distribution of points after transformation by T . If the density $f(x)$ is invariant, then by definition

$$\int_a^b f(s) ds = \int_{T^{-1}([a,b])} f(s) ds \tag{7}$$

for each $[a, b] \subset [0, L]$. However, from (5) equation (7) may be rewritten as

$$\int_a^b f_1(s) ds = \int_a^b f(s) ds \tag{8}$$

and thus, if the density $f(x)$ is invariant, then $f_1(x) = f(x)$. By induction, $f_n(x) = f(x)$ for any number of iterations of the transformation $T(x)$.

The second notion concerning densities which must be introduced is that of stability. An invariant density $f(x)$ is said to be *stable* (asymptotically) if, for any other density $g(x)$,

$$\int_{T^{-n}([a,b])} g(s) ds \rightarrow \int_a^b f(s) ds \tag{9}$$

for each $[a, b] \subset [0, L]$ as $n \rightarrow \infty$.

Thus, if the N points are initially distributed on $[0, L]$ according to $g(x)$, after transformation by $T(x)$ they will have a distribution $g_1(x)$. After n transformations, the distribution will be $g_n(x)$, and by induction

$$\int_a^b g_n(s) ds = \int_{T^{-n}([a,b])} g(s) ds. \tag{10}$$

Stability of $f(x)$ requires, by definition, that the right-hand side of (10) approach $\int_a^b f(s) ds$, or that

$$\int_a^b g_n(s) ds \rightarrow \int_a^b f(s) ds. \tag{11}$$

Thus if $f(x)$ is a stable distribution, then for any other initial distribution $g(x)$, the successive distributions $g_n(x)$ resulting from n applications of T will satisfy (11) as n tends to infinity.

The following theorem summarizes the results of Ruelle (1977) and Pianigiani (1979b) on the existence of a stable invariant density for transformations T with certain properties.

Theorem 1. *Let $T: [0, L] \rightarrow [0, L]$ be twice differentiable, $T(0) = T(L) = 0$, and assume that $T(x)$ has a unique maximum at $c \in (0, L)$ such that $T(c) = L$. If there is a positive integrable function $h(x)$ such that*

$$r_h(x) \doteq \frac{h(x)}{|T'(x)|h(T(x))} \leq \mu < 1, \quad \mu > 0$$

for all $x \in (0, L)$, $x \neq c$, and the derivative $dr_h(x)/dx$ exists and is bounded, then there is a density $f(x)$ that is stable and invariant with respect to the transformation T .

Remark. Although neither Pianigiani nor Ruelle considered the stability of the invariant density, stability follows from the fact that the transformation $S = HTH^{-1}$, where $H(x) = Q \int_0^x h(s) ds$, $Q = L[\int_0^L h(s) ds]^{-1}$, is mixing (Rochlin, 1964).

III. The Extinction of Slowly Evolving Systems

Consider a system whose evolution in time is described by the sequence of state variables $x_0, x_1, \dots, x_i, \dots$. The successive values of the state variables x are due to the operation of a transformation $T(r, x)$, where r is a parameter that changes slowly with time. Thus, given an initial point x_0 and taking $r = r_0 + i\varepsilon$, the sequence of state variables describing the system becomes $x_0, x_1 = T(r_0 + \varepsilon, x_0), \dots, x_i = T(r_0 + i\varepsilon, x_{i-1}), \dots$.

It is assumed that $T(r, x)$ is defined on $[0, L_r]$, and that:

- 1) $T(r, 0) = T(r, L_r) = 0$ for all r .
- 2) $T(\tilde{r}, c_{\tilde{r}}) = \max_x T(r, x) \begin{cases} < L_r & \text{for } r < \tilde{r}, \\ = L_r & \text{for } r = \tilde{r}, \\ > L_r & \text{for } r > \tilde{r}. \end{cases}$
- 3) $\frac{\partial T}{\partial r} \Big|_{(\tilde{r}, c_{\tilde{r}})} > \frac{dL_r}{dr} \Big|_{\tilde{r}}$ and $\frac{\partial^2 T}{\partial x^2} \Big|_{(\tilde{r}, c_{\tilde{r}})} < 0$.
- 4) $T(\tilde{r}, x)$ has a unique stable invariant density $f(x)$.

If at any point in time $x_i \notin [0, L_{r_0+i\epsilon}]$, then the sequence of points terminates because x_{i+1} is undefined as are all subsequent values of the state variable. When this occurs, the system is said to be extinct. With two different initial conditions for the system extinction may occur at quite different times even though all other factors are equal. Our problem is to determine the asymptotic distribution of the times at which system extinction occurs.

Extinction of the system will not be possible until $r_0 + i\epsilon \geq \tilde{r}$, and thus the origin of the extinction times k is taken to be such that $k = 0$ when $r = \tilde{r}$. For $k > 0$, $r = \tilde{r} + k\epsilon$. Suppose that, at $r = \tilde{r}$, there are N points distributed on $[0, L_{\tilde{r}}]$ with the stable invariant density $f(x)$. We assume that ϵ is so small that the product (ϵk^3) remains bounded for all k of interest. [The reason we have assumed that (ϵk^3) is bounded will become clear from the following arguments.] Though the density $f(x)$ is invariant with respect to $T(\tilde{r}, x)$, it is not necessarily invariant with respect to $T(\tilde{r} + k\epsilon, x)$. However, it can be calculated that after k iterations (with ϵk^3 bounded) the change in the density $f(x)$ is of the order $\epsilon^{1/3}$ in a neighborhood of $x = c_{\tilde{r}}$. Thus in our computations we may use the $f(x)$ invariant with respect to $T(\tilde{r}, x)$ in calculating the distribution of extinction times.

Suppose that after k iterations, the number of the initial N points remaining (i.e., those which have not become extinct) is $N_k \leq N$. Now

$$N_k - N_{k+1} = N_k \int_{B_k} f(x) dx \tag{12}$$

where $B_k = \{x: T(\tilde{r} + k\epsilon, x) > L_{\tilde{r} + k\epsilon}\}$. A rather elementary calculation involving the expansion of $T(\tilde{r} + k\epsilon, x)$ about $(\tilde{r}, c_{\tilde{r}})$ and the expansion of $L_{\tilde{r} + k\epsilon}$ about \tilde{r} and neglecting terms of order $\epsilon^{3/2}$ and higher defines the set B_k as

$$c_{\tilde{r}} - \sqrt{\frac{2(q_1 - q_2)k\epsilon}{|T''_x|}} \lesssim x \lesssim c_{\tilde{r}} + \sqrt{\frac{2(q_1 - q_2)k\epsilon}{|T''_x|}}$$

where $q_1 = (\partial T/\partial r)_{(\tilde{r}, c_{\tilde{r}})}$, $q_2 = (dL_r/dr)_{\tilde{r}}$, and $T''_x = (\partial^2 T/\partial x^2)_{(\tilde{r}, c_{\tilde{r}})}$. Thus (12) becomes

$$\begin{aligned} N_k - N_{k+1} &\simeq |B_k|f(c_{\tilde{r}}) \\ &= N_k M \sqrt{k\epsilon} f(c_{\tilde{r}}) \end{aligned} \tag{13}$$

where

$$M = 2 \sqrt{\frac{2(q_1 - q_2)}{|T''_x|}}$$

From (13),

$$N_{k+1} \simeq N_k [1 - Mf(c_{\tilde{r}})\sqrt{k\epsilon}]$$

so

$$N_k \simeq N \exp \left[- \sum_{i=1}^k M \sqrt{i\epsilon} f(c_{\tilde{r}}) \right]. \tag{14}$$

Using $\sum_{i=1}^k \sqrt{i\epsilon} = 2k\sqrt{k\epsilon}/3 + 0(\epsilon^{1/3})$, (14) becomes

$$N_{k+1} = N \exp(-\sigma\sqrt{\epsilon} k^{3/2}) \tag{15}$$

where $\sigma = 2Mf(c_{\tilde{r}})/3$. Equation (15) is the main result of this section, and allows the probability of survival to time k , $p_k = N_k/N$, to be written as

$$p_{k+1} = \exp(-\sigma\sqrt{\varepsilon} k^{3/2}). \tag{16}$$

From (15) and (16), it is clear why we have restricted our considerations to $(\sqrt{\varepsilon} k^{3/2})^2 = (\varepsilon k^3)$ bounded.

Although (15) and (16) were derived under the assumption that the initial distribution $f(x)$ was invariant, since ε is small by assumption the formulae are valid for any arbitrary initial distribution $g(x)$. This is because $f(x)$ is, by assumption 4, stable and thus for any initial distribution $g(x)$ the sequence $g_k(x)$ converges rapidly (in comparison with the extinction process) to $f(x)$.

IV. The Slowly Evolving Quadratic Map

As an example of the application of the results on system extinction developed in the previous section, consider the slowly evolving quadratic system defined by (1), so

$$x_{k+1} = (\tilde{r} + k\varepsilon)x_k(1 - x_k). \tag{17}$$

Clearly for $T(r, x) = rx(1 - x)$, $T(r, 0) = T(r, 1) = 0$, and $T(4, \frac{1}{2}) = 1$ so $\tilde{r} = 4$ and $c_{\tilde{r}} = \frac{1}{2}$. The density for (1) when $r = 4$ is known exactly (Ulam and von Neumann, 1947) and is

$$f(x) = \frac{1}{\pi\sqrt{x(1-x)}}. \tag{18}$$

It is a simple matter to show that the conditions of Theorem 1 are exactly satisfied with

$$h(x) = \frac{1}{\sqrt{x(1-x)}} \tag{19}$$

and the density $f(x)$ is thus stable and invariant.

A few simple calculations give $q_1 = \frac{1}{4}$, $q_2 = 0$, $T'''(\tilde{r}, c_{\tilde{r}}) = -8$, and $f(\frac{1}{2}) = 2/\pi$ so the expression for the probability of survival to time k becomes

$$P_{k+1} = \exp[-(\frac{2}{3}\pi)\sqrt{\varepsilon} k^{3/2}]. \tag{20}$$

Figure 1 displays two trajectories for the system

$$x_{i+1} = (r_0 + k\varepsilon)x_i(1 - x_i) \tag{21}$$

computed with $r_0 = 2.8$, $\varepsilon = 0.01$, and assuming two different initial values of x_0 . These trajectories display a fascinating complexity which is, however, understandable from previous characterizations of the behaviour of (1) for various values of the parameter r . For $r < 3.0$, the fixed point $(r - 1)/r$ is stable, though increasing slowly, and the computed trajectories display a damped approach to the slowly increasing fixed point. This region corresponds to times $i < 20$. Once $r = 3.0$, at $i = 20$, the fixed point is no longer stable and the trajectories start to oscillate and as

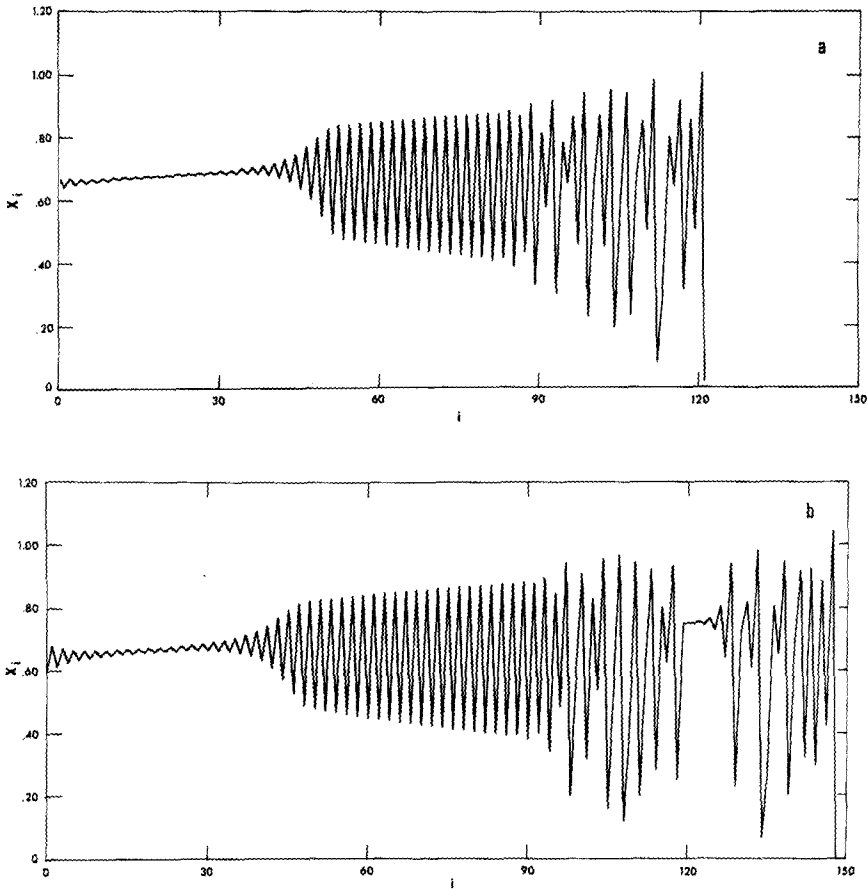


Fig. 1. Two trajectories for the system (21), with $r_0 = 2.8$, $\varepsilon = 0.01$, illustrating the effect of the initial condition x_0 on the dynamics and the time of extinction. For the system at the top, $x_0 = 0.38$, while in the bottom panel $x_0 = 0.36$

time progresses the amplitude of these oscillations also increases in response to the increase in r . Eventually, the trajectories become chaotic [cf. Li and Yorke (1975), Pianigiani (1979a), Ruelle (1977)], and it is only once this region has been reached that there is any significant difference in the behaviour of trajectories starting from different initial conditions. Once $r = 4$ at $i = 120$ the system is now capable of displaying behaviour not available for $r < 4$; namely, it will become extinct. In the top trajectory of Fig. 1, with $x_0 = 0.36$, this extinction occurs after only 121 ($k = 1$) iterations, while in the bottom trajectory ($x_0 = 0.38$) it takes 148 steps ($k = 28$) for extinction to take place.

Several experimentally determined distributions of survival times derived from a number of trajectories are shown in Fig. 2. A sequence of iterates was computed from (17) with $r_0 = 4$, $\varepsilon = 0.01$, and a uniform distribution of initial conditions $x_0 \in (0, 1)$. The solid line is the survival probability expected on the basis of equation (20), while the filled and open circles and the crosses are, respectively, the survival probabilities determined for 50, 100, and 200 different initial conditions.

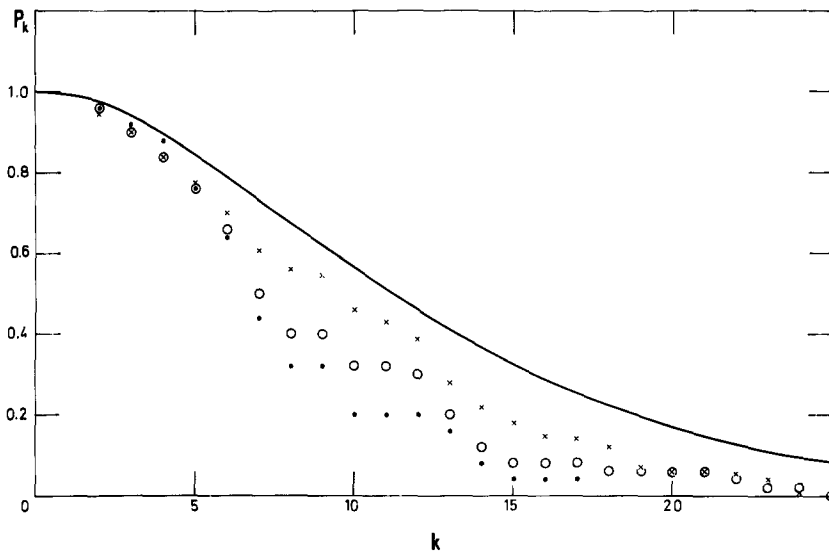


Fig. 2. The probability of survival of the system (21), with $r_0 = 2.8$, $\varepsilon = 0.01$. The solid curve gives the theoretically expected result as predicted by (20). The points marked by \bullet , \circ , and \times give, respectively, the numerically generated results with 50, 100, and 200 different initial conditions x_0 uniformly distributed on $(0, 1)$

V. A Renewing Cell Population

As a second example of the application of the results of section III, here we consider the dynamics of a simple model for a renewing, self-maintaining, cellular population with a progressive increase in the cellular production rate. This example is of interest in that it illustrates the nature of the extinction process for a system described by an asymmetric transformation, and for which the interval length L varies.

Consider a population N of cells which die, or differentiate, at a rate δ and which are produced at a rate β . The population is characterized by some basic time unit τ , and between successive times t_i and $t_i + \tau$ the change in cell numbers is given by

$$N_{i+1} - N_i = N_i(\beta - \delta)\tau. \quad (22)$$

It is assumed that the population is self-maintaining by virtue of a cellular production rate dependent on cellular numbers according to

$$\beta = \beta_m \frac{\Theta}{\Theta + N} \quad (23)$$

where β_m is the maximal cell production rate and Θ is a parameter. Thus the complete population dynamics are controlled by

$$N_{i+1} = N_i \left\{ (1 - \delta\tau) + \beta_m\tau \frac{\Theta}{\Theta + N_i} \right\}. \quad (24)$$

Chronic myelogenous leukemia (CML) is a neoplastic disorder of the hemato-poietic system characterized by a progressive increase in the number of circulating white blood cells. There is strong evidence (Wintrobe, 1976) for the clonal origin of CML, with the basic defect probably resident in the uncommitted stem cell population. In examining the available cell kinetic data in CML patients, one interpretation (Mackey, 1979) is that the defect is expressed as an inexorable increase in the maximum cell production rate within the stem cell compartment. If this is indeed the case, then the model of this section offers a highly simplified paradigm for the behaviour of the stem cell population in CML. To examine the nature of extinction in the model system (24) assume that the maximal production rate β_m increases in the manner

$$\beta_m = \beta_0 + i\varepsilon.$$

Since Θ simply scales the N_i without playing any role in determining the dynamics it is convenient to set $x_i = N_i/\Theta$ so

$$\begin{aligned} x_{i+1} &= x_i \left[-A + \frac{B}{1+x_i} \right] \\ &= T(B, x_i) \end{aligned} \tag{25}$$

where $A = \delta\tau - 1$, and $B = (\beta_0 + i\varepsilon)\tau$. A few elementary calculations show that $T(B, 0) = T(B, L_B) = 0$ where $L_B = (B/A) - 1$. Further, with $A > 1$, $\tilde{B} = A(A+1)^2/(A-1)^2$ and $c_{\tilde{B}} = 2/(A-1)$ so $T(\tilde{B}, c_{\tilde{B}}) = L_{\tilde{B}}$. Although the density $f(x)$ is not known analytically for (25), with

$$h(x) = \frac{1}{\sqrt{x(L_B - x)}}$$

it may be shown that the conditions of Theorem 1 are satisfied for all $A > 1$. Thus conditions 1 through 4 of section III are satisfied for (25) when $A > 1$.

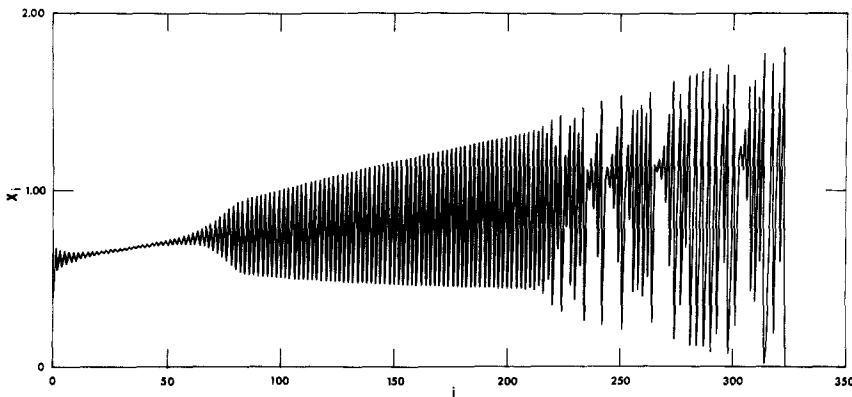


Fig. 3. This figure illustrates the evolution and extinction of the system (25) with $A = 4.0$, $B_0 = 8.0$, $\varepsilon\tau = 0.01$, and $x_0 = 0.10$

To calculate the probability of survival of the system (25) once $B > \tilde{B}$, note that $q_1 = 2/(A + 1)$, $q_2 = 1/A$, $T''(\tilde{B}, c_{\tilde{B}}) = -2A(A - 1)/(A + 1)$, and thus $M = 2/A$. The final quantity necessary to calculate the probability of survival to time k for the system (25) is the density $f(c_{\tilde{B}})$. Although this cannot be calculated analytically, it can be calculated numerically given A . For $A = 4$, $\tilde{B} = 100/9$, $c_{\tilde{B}} = \frac{2}{3}$, and $f(\frac{2}{3}) \approx 0.37$.

Figure 3 shows a trajectory for the system (25) computed with $A = 4$, $B = B_0 + i\epsilon\tau$, $B_0 = 8$, and $\epsilon\tau = 0.01$. The qualitative behaviour is very similar to that displayed by (17). It is only when $i \approx 311$ that $B = \tilde{B}$ and that extinction is a possibility. In Fig. 3, extinction occurs for $k = 27$.

Figure 4 shows the results of a number of numerical experiments on the system (25). A sequence of iterates was computed with $A = 4$, $B = 100/9$, $\epsilon\tau = 0.01$, and a uniform distribution of initial conditions on $(0, 100/9)$. The theoretical results expected on the basis of (16) are indicated by the solid line, while the other symbols give the results of numerical calculations based on 50, 100, and 200 initial points uniformly distributed on the interval.

A number of studies have examined the survival statistics in groups of CML patients, and these results are most interesting within the context of this paper. In every case with which we are familiar, probability of survival a length of time t from diagnosis follows a distribution of the form $p(t) = \exp(-\alpha t^n)$, with $n \approx 1.5$. Thus the data of Shimkin et al. (1950) gives $\alpha = 0.14$, $n = 1.56$; while the data of Wintrobe (1976) yields $\alpha = 0.16$, $n = 1.51$. For the systems considered in this paper, $n = \frac{3}{2}$ [cf. equation (16)]. We speculate that the close correspondence between the statistical survival curves for groups of CML patients, and the predictions of equation (16) for the extinction of slowly evolving dynamical systems presented here is not fortuitous. We suspect that death in CML patients may be a result of an

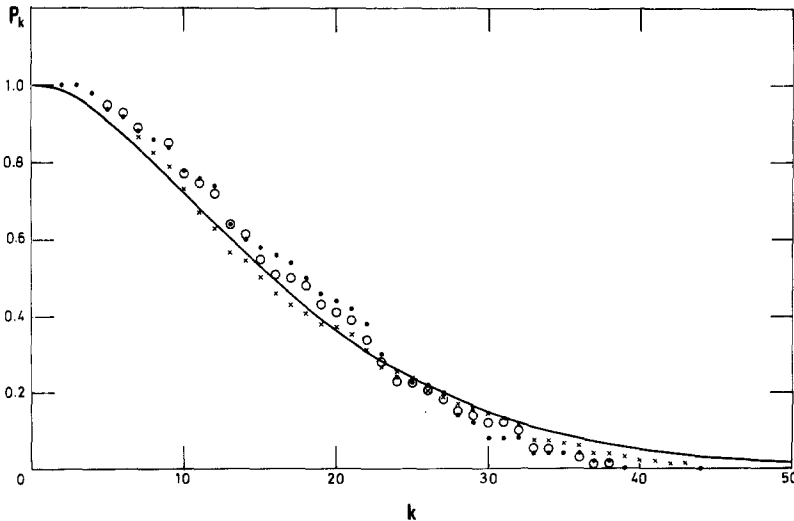


Fig. 4. The survival probability of the system (25) with $A = 4.0$, $B_0 = 8$, $\epsilon\tau = 0.01$. Symbols as in Fig. 2, with initial conditions distributed uniformly on $(0, 100/9)$

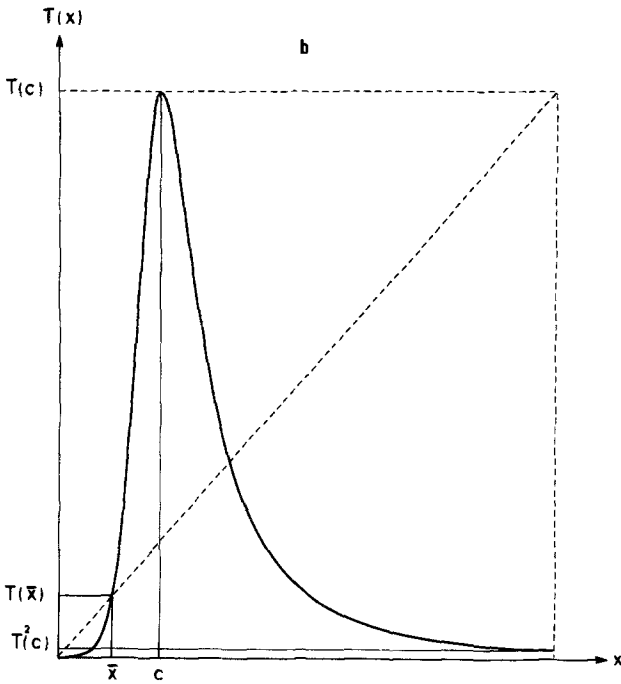
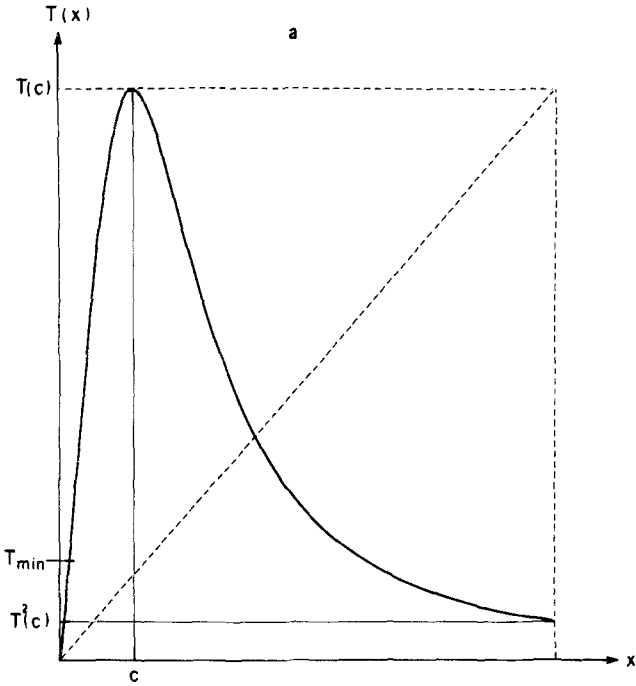


Fig. 5. This illustrates two other types of transformations for which the extinction considerations of this paper are applicable. See the Discussion for details

extinction process similar to that outlined in section III, and which the simple paradigm for a renewing cell population presented here displays as the maximum cell production rate increases. With respect to the behaviour of (25) illustrated in Fig. 3, it is also interesting to note that some CML patients display marked oscillations in their circulating white blood cell count that is also reflected in more primitive precursor cells in the marrow (cf. Mackey, 1979).

Interestingly enough, CML survival curves seem to be relatively unaffected by the use of various therapeutic measures. Given the fact that these measures involve the use of cytostatic tools (drugs or radiotherapy), and that the utilization of these will have the effect of resetting the levels of proliferating cellular populations, if CML evolves in a fashion similar to (25) then the lack of effect of these therapies on population survival statistics is totally understandable within the context of the considerations here. Although these therapies currently employed may have no effect on the survival characteristics of a *population*, if death in CML is due to an extinction process as outlined here it is clear that the use of drugs may have a dramatic effect on lifespan for an *individual*. Specifically, in a given patient the results of this paper indicate that therapy may dramatically shorten *or* prolong their lifespan.

V. Discussion

In the preceding sections we have presented a simple formulation within which extinction processes in simple dynamical systems may be considered. Although the procedure was illustrated with two examples in which extinction occurs because a state variable becomes negative, it may be extended to at least two other deterministic situations, touched on by May and Oster (1976), in which extinction takes place by slightly different means.

In the first situation, consider that the population dynamics are evolving according to $x_{i+1} = T(r_i, x_i)$ and that T is a regular, non-negative convex function with a single maximum at $x = c$ (cf. Fig. 5a). In this case extinction may occur if the transformation is sufficiently steep such that $T^2(c)$ falls below a certain value corresponding to the minimum number of biological units necessary for reproduction, e.g., two for organisms reproducing bisexually.

A second example (cf. Fig. 5b) in which extinction may take place is one in which an Allee effect (Watt, 1964) alters the dynamics of Fig. 5a to produce a third fixed point \bar{x} . In this case, if $T^2(c) < T(\bar{x})$ then the system will also eventually become extinct. In both of these examples if the systems are evolving slowly, the results of section III, with appropriate changes of variables, may be used to examine the extinction process.

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