

Stability in Discrete Population Models

P. Cull* and J. Chaffee^{† 1}

* *Computer Science Dept., Oregon State University, Corvallis, OR 97331 USA, pc@cs.orst.edu*

[†] *Mathematics Dept., Western Washington University, Bellingham, WA 98225 USA.*

Abstract. One dimensional nonlinear difference equations have been used to model population growth. The standard biological models have the interesting characteristic that they display global stability if they display local stability. Various researchers have sought a simple explanation for this agreement of local and global stability. Here, we show that enveloping by a linear fractional function is sufficient for global stability. We also show that for seven standard biological models local stability implies enveloping and hence global stability. We derive two methods to demonstrate enveloping and show that these methods can easily be applied to the seven example models.

Keywords: population models, growth models, stability, local stability, global stability, linear fractional functions, difference equations, recurrences, maps of the interval, chaos

INTRODUCTION

Simple population growth models have a pleasant property, they display global convergence if they have local convergence. This fact was established for a number of models by Fisher et al [FGV79,Goh79] who constructed an explicit Lyapunov function for each model they studied. Since then a number of workers have created a variety of sufficient conditions to demonstrate global stability. [Sin78,Ros83,Cul88b,Cul86,Cul81,Cul88a] Each of these methods suffer from the difficulty that either the method does not apply to one of the commonly used models or the method is computationally difficult to apply.

In this paper, we describe a simple condition which is satisfied by all the commonly used simple population models, and we show that for these models the computation for the method is not difficult. Our simple condition is that the population models are *enveloped* by *linear fractional functions*. No single linear fractional serves for all models. Instead the linear fractionals depend on a single parameter which must be adjusted for the particular model. In some cases,

¹) Supported in part by NSF Grant DMS 9531576

this parameter will also change depending on the parameters of the model. This parameter dependence may be why this simple condition has not been discovered before.

Our pleasure with this result is not solely mathematical. There is also a psychological component. We suspect that the original creators of these models were good biologists and not sophisticated mathematicians. If the similarity among these models required deep and complicated mathematics, we would feel that we had not captured the simple vision of the original modelers. We will argue that the usual way of writing these models suggests an implicit constraint that will force enveloping by a linear fractional.

Further, we also mention a result noted by Singer [Sin78] and Cull [Cul88b] that the usual models are *buffered*, that is, making the model slightly more complicated will *not* change the local stability implies global stability result. On the other hand, we mention that it is trivial for a mathematician to create more complicated models in which either the enveloping or the local implies global result do not hold.

SIMPLE POPULATION MODELS

The simplest difference equation model for population growth is

$$x_{t+1} = rx_t$$

where x_t is a measure of the population size at time t , and r is a growth rate. Much of biological reality has been stripped from this model. For example, individuals, sexes, ages, and spatial distribution have all been ignored. On the other hand, this simple model may make useful predictions in certain circumstances. For example, when a new species is introduced into or invades a favorable environment, the growth of the introduced species may initially follow this simple model. For longer range predictions this model is untenable, since it predicts that

$$x_t = r^t x_0$$

and such exponential growth cannot be sustained. (Although there is some question about whether the human population is still showing exponential growth.)

More reasonable models assume that the growth rate decreases with the population size. For example, the quadratic model

$$x_{t+1} = x_t[1 + (r - 1)(1 - x_t/K)]$$

is often used. Here the growth rate is r when x is small and if x reaches K , then the rate becomes 1 and one may hope that the population size will stay at K . By the way, K is called the carrying capacity since if x is below K the population is increasing, while if x is above K the population is decreasing. One might guess that regardless of the initial population size, this model would predict that the population size would eventually approach K . This guess can be supported by the observation that this discrete time model is analogous to the differential equation

$$dx/dt = x(r - 1)(1 - x/K)$$

and it can obviously be argued that as long as $r > 1$ and the initial population size $x(0)$ is positive then $\lim_{t \rightarrow \infty} x(t) = K$. This convergence follows because $x(t)$ is restricted to smooth evolution on the line. So $x(t)$ cannot jump and, in particular, $x(t)$ cannot jump over K . Here if $x(0) < K$ then $x(t)$ is monotonically increasing toward K , while if $x(0) > K$ then $x(t)$ is monotonically decreasing toward K .

But things are not so simple when one considers the difference equation rather than the differential equation. At least from the time of Euler, it has been known that one must choose the step size small enough for the difference equation to behave like the differential equation. In particular, as x approaches K , one must make the step size small enough to prevent x from jumping over K . This choice of step size would result in a rescaled smaller r being used in the difference equation. Clearly, this rescaling is simply an inconvenience if one is considering the the differential equation as the real model and the difference equation as merely a computational approximation to the real model. But, if one accepts the difference equation as the real model, then jumping over K is a phenomenon which cannot be ignored. Luckily, in this example, if r is small, nothing too dreadful happens. The solution to the difference equation jumps back and forth over K , but in the long run the solution approaches K , as one would have predicted from the differential equation. Convergence is not lost, but monotonicity is lost.

This description of the relation between differential and difference equations would have been satisfactory to most modelers 30 years ago, but things changed in the '70s. In particular, May's [May74, May76] examples demonstrated that difference equations had more complicated behavior than differential equations. Instead of simple convergence, difference equations displayed wild cycles and a phenomenon which Li and Yorke [LY75] called *chaos*. Figure 1 shows the time trajectory of a difference equation in the chaotic regime. Figure 2 shows a phase portrait of this trajectory. This paper will not focus on chaos. We refer the interested reader to the introductory text by Devaney [Dev86]. Instead, we will study the convergence behavior of difference equation models.

Since the differential equation models converge to K regardless of the starting point, we will call such a model *globally stable*. For difference equations, we could have oscillations for essentially all starting points, or we could have convergence to K for starting points close to K and have oscillations for starting points far from K , or we could have convergence to K for all starting points. We distinguish these three situations as *oscillation*, *local stability*, and *global stability*. We want to focus on a strange but interesting observation: for all the simple population models from the literature, local stability implies global stability. The question we seek to answer is: What property do these models have in common that causes local stability to imply global stability?

We and others have investigated this question of global stability. As we will see a variety of analysis methods have been proposed, but they were all in some sense unsatisfactory. An ideal method should be strong enough to apply to all the models we will study, and be easy to apply to these models. Further, the ideal method should be psychologically satisfying in that it should explain how mathematically unsophisticated biologists could produce models in which local stability implies global stability. This could be most easily done, if one could come up with some sense of *simple* or *smooth* that applies to all the example models. In this paper, we give our solution: The example models are *well-behaved* in the sense that each can be *enveloped* by a simple kind of function, a linear fractional function.

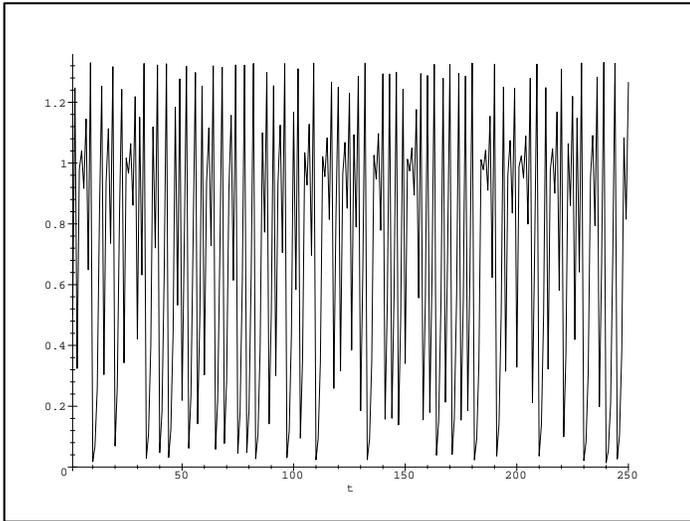


FIGURE 1. Time Plot of Model II with $r=2.99$, showing chaotic behavior .

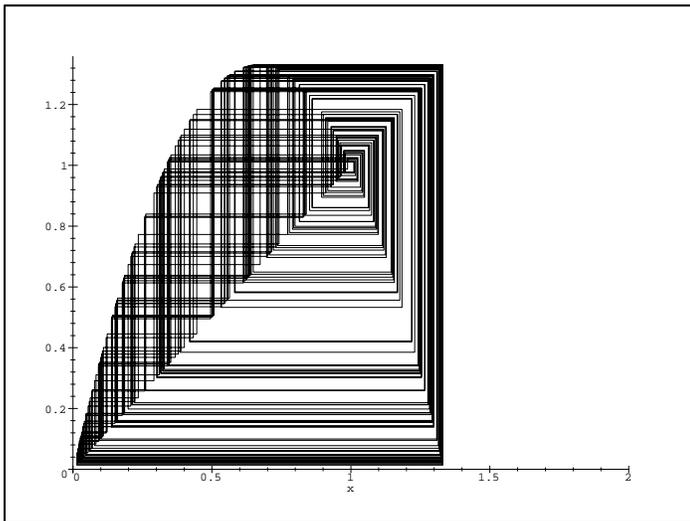


FIGURE 2. Phase Plane Plot of Model II with $r=2.99$, showing chaotic behavior .

The rest of this paper is organized so that Section 3 gives historical background and the necessary definitions, Section 4 proves our theorems, Section 5 applies our theorems to the example models, and Section 6 closes with a short discussion.

BACKGROUND AND DEFINITIONS

In the most general sense, we want to study difference equations of the form

$$x_{t+1} = f(x_t)$$

but with this degree of generality, little can be said. If we require that f is a function which is defined for all values of x , then given an initial condition x_0 , we can show that there is a unique solution to the difference equation, that is, x_t traces out a well-defined trajectory. To obtain stronger results, we will assume that f is continuous and has as many continuous derivatives as necessary. As we will see in the examples, we will assume even more structure for a population model. Intuitively, if there is no population now, there will be no population later. If the population is small, we expect it to be growing. If the population is large, we expect it to be decreasing. These ideas suggest that there should be an *equilibrium point* where the population size will remain constant. We expect the function f to be *single-humped*, that is, f should rise to a maximum and then decrease. For some models, f will go to 0 for some finite x , but for other models f will continually decrease toward 0.

We sum up these observations with the following definition.

A **population model** is a difference equation of the form

$$x_{t+1} = f(x_t)$$

where f is a continuous function from the nonnegative reals to the nonnegative reals and there is a positive number \bar{x} , the equilibrium point, such that:

$$f(0) = 0$$

$$f(x) > x \quad \text{for } 0 < x < \bar{x}$$

$$f(x) = x \quad \text{for } x = \bar{x}$$

$$f(x) < x \quad \text{for } x > \bar{x}$$

and if $f'(x_m) = 0$ and $x_m \leq \bar{x}$ then

$$f'(x) > 0 \quad \text{for } 0 \leq x < x_m$$

$$f'(x) < 0 \quad \text{for } x > x_m \text{ such that } f(x) > 0.$$

We will allow the possibility that $f(x) = 0$ for all $x > x_\infty$ and therefore, that $f(x)$ is not strictly differentiable at x_∞ . Otherwise, we assume that f is three times continuously differentiable.

We want to know what will happen to x_t for large values of t . Clearly we expect that if x_0 is near \bar{x} then x_t will overshoot and undershoot \bar{x} . Possibly this oscillation will be sustained, or

possibly x_t will settle down at \bar{x} . The next definitions codify these ideas. A population model is **globally stable** if and only if for all x_0 such that $f(x_0) > 0$ we have

$$\lim_{t \rightarrow \infty} x_t = \bar{x}$$

where \bar{x} is the unique equilibrium point of $x_{t+1} = f(x_t)$. A population model is **locally stable** if and only if for every small enough neighborhood of \bar{x} if x_0 is in this neighborhood, then x_t is in this neighborhood for all t , and

$$\lim_{t \rightarrow \infty} x_t = \bar{x}.$$

How can we decide if a model has one of these properties? The following well-known theorem gives one answer.

Theorem 1 *If $f(x)$ is differentiable then, a population model is locally stable if $|f'(\bar{x})| < 1$, and if the model is locally stable then $|f'(\bar{x})| \leq 1$.*

For global stability, a slight modification of a very general theorem of Sarkovskii [Sar64] gives:

Theorem 2 *A continuous population model is globally stable iff it has no cycle of period 2. (That is, there is no point except \bar{x} such that $f(f(x)) = x$.)*

This theorem has been noted by Cull [Cul81] and Rosenkranz [Ros83].

Unfortunately, this global stability condition may be difficult to test. Further, there is no obvious connection between the local and global stability conditions.

Various authors have demonstrated global stability for some population models. Fisher *et al* [FGV79] and Goh [Goh79] used Lyapunov functions [LaS76] to show global stability. This technique suffers from the drawbacks that a different Lyapunov function is needed for each model and that there is no systematic method to find these functions. Singer [Sin78] used the negativity of the Schwarzian to show global stability. This technique does not cover all the models we will consider, and it even requires modification to cover all the models it was claimed to cover. Rosenkranz [Ros83] noted that no period 2 was implied by $|f'(x)f'(f(x))| < 1$ and showed that this condition held for a population genetics model. This condition seems to be difficult to test for the models we will consider. Cull [Cul81, Cul86, Cul88b, Cul88a] developed two conditions **A** and **B** and showed that each of the models we will consider satisfied at least one of these conditions. These conditions used the first through third derivatives and so were difficult to apply. Also, as Hwang [Hua86] pointed out these conditions required continuous differentiability. All of these methods are relatively mathematically sophisticated, and so it is not clear how biological modelers could intuitively see that these conditions were satisfied.

If we return to the condition for local stability, we see that it says if for x slightly less than 1, $f(x)$ is below a straight line with slope -1 , and if for x slightly greater than 1, $f(x)$ is above the same straight line, then the model is locally stable. If we consider the model

$$x_{t+1} = x_t e^{2(1-x_t)},$$

we can see that the local stability bounding line is $2 - x$. Somewhat suprisingly, this line is an upper bound on $f(x)$ for all x in $[0, 1)$ and a lower bound for all $x > 1$. Since $2 - (2 - x) = x$, the bounding by this line can be used to argue that for this model there are no points of period 2, and hence the model is globally stable. From this example, we abstract the following definition. A function $\phi(x)$ *envelops* a function $f(x)$ if and only if

- $\phi(x) > f(x)$ for $x \in (0, 1)$
- $\phi(x) < f(x)$ for $x > 1$ such that $\phi(x) > 0$ and $f(x) > 0$

We will use the notation $\phi(x) \bowtie f(x)$ to symbolize this enveloping.

As we will see, our example population models have one or more parameters, and a model with one choice of parameters will envelop the same model with a different choice of parameters. For example, the function $xe^{2(1-x)}$ envelops all the functions of the form $xe^{r(1-x)}$ for $r \in (0, 2)$.

While a straight line was sufficient to envelop $xe^{2(1-x)}$, a straight line fails to envelop the closely related function $x[1 + 2(1 - x)]$. To get a more general enveloping function, we consider the ratio of two linear functions and assume that the ratio is 1 when $x = 1$ and the derivative of this function is -1 when $x = 1$, which gives the following definition.

A **linear fractional function** is a function of the form

$$\phi(x) = \frac{1 - \alpha x}{\alpha - (2\alpha - 1)x} \quad \text{where } \alpha \in [0, 1) .$$

These functions have the properties

- $\phi(1) = 1$
- $\phi'(1) = -1$
- $\phi(\phi(x)) = x$
- $\phi'(x) < 0$.

The shape of our linear fractional functions changes markedly as α varies. For $\alpha = 0$, $\phi(x) = 1/x$, which has a pole at $x = 0$, and decreases with an always positive second derivative. For $\alpha \in (0, 1/2)$, $\phi(x)$ starts (for $x = 0$) at $1/\alpha$ and decreases with a positive second derivative. For $\alpha = 1/2$, $\phi(x) = 2 - x$, which starts at 2 and decreases to 0 with a zero second derivative. For $\alpha \in (1/2, 1)$, $\phi(x)$ starts at $1/\alpha$, decreases with a negative second derivative, and hits 0 at $1/\alpha$ which is greater than 1. We are only interested in these functions when $x > 0$ and $\phi(x) > 0$, so we do not care about the pole in these linear fractionals because the pole occurs outside the area of interest.

Figure 3 shows the various forms of our linear fractional functions.

THEOREMS

We are now in a position to prove the necessary theorems. In what follows, we will assume that our model is $x_{t+1} = f(x_t)$, and that the model has been normalized so that the equilibrium

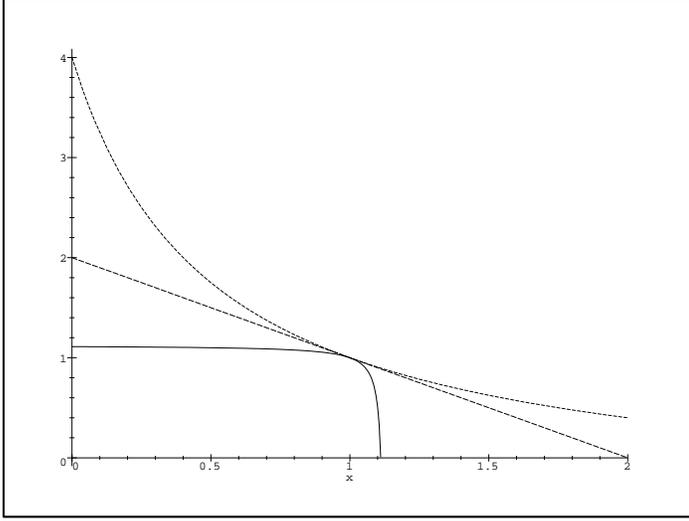


FIGURE 3. Three linear fractional functions, $\alpha = \frac{1}{4}$, $\alpha = \frac{1}{2}$, $\alpha = .9$.

point is 1, that is $f(1) = 1$. We will use the notation $f^k(x)$ to mean that the function f has been applied k times to x . This notation can be recursively defined by $f^0(x) = x$ and $f^i(x) = f(f^{i-1}(x))$ for $i \geq 1$.

Theorem 3 *Let $\phi(x)$ be a monotone decreasing function which is positive on $(0, x_-)$ and so that $\phi(\phi(x)) = x$. Assume that $f(x)$ is a continuous function such that:*

- $\phi(x) > f(x)$ on $(0, 1)$
- $\phi(x) < f(x)$ on $(1, x_-)$
- $f(x) > x$ on $(0, 1)$
- $f(x) < x$ on $(1, \infty)$
- $f(x) > 0$ on $(1, x_\infty)$

then for all $x \in (0, x_\infty)$, $\lim_{k \rightarrow \infty} f^k(x) = 1$.

Proof. From Sarkovskii's theorem, it suffices to show that $f(x)$ has no cycle of period 2. We show that $f(f(x)) > x$ for $x \in (0, 1)$. If $f(f(x)) > 1$ then $f(f(x)) > x$. If $f(f(x)) < 1$ and $f(x) < 1$ then $f(f(x)) > f(x) > x$. If $f(f(x)) < 1$ and $f(x) > 1$, $\phi(f(x)) < f(f(x))$ and $x_- > \phi(x) > f(x)$, and since $\phi(x)$ is decreasing and self inverse $x = \phi(\phi(x)) < \phi(f(x)) < f(f(x))$.

A similar argument shows that $x > f(f(x))$ for $x > 1$. (Even if $f(x) > 1$, $f(x) < x_-$ because $x_- > \phi(x)$.) Even though Sarkovskii's theorem assumes a closed interval, we are showing that there are no cycles in an open interval, and so none within the closed intervals inside the open interval. Further our assumptions on $f(x)$ allow us to argue that there is a small ε so that $f^k(x)$ will eventually fall into the the closed interval $[\varepsilon, \phi(\varepsilon)]$. \square

A slight recasting of the above argument gives:

Corollary 1 *If $f_1(x)$ is enveloped by $f_2(x)$, and $f_2(x)$ is globally stable, then $f_1(x)$ is globally stable.*

Corollary 2 *If $f(x)$ is enveloped by a linear fractional function then $f(x)$ is globally stable.*

A function $h(z)$ is **doubly positive** iff

1. $h(z)$ has a power series $\sum_{i=0}^{\infty} h_i z^i$
2. $h_0 = 1, h_1 = 2$
3. For all $n \geq 1$ $h_n \geq h_{n+1}$
4. For all $n \geq 2$ $h_n - 2h_{n+1} + h_{n+2} \geq 0$

Theorem 4 *Let $x_{t+1} = f(x_t)$ where $f(x) = xh(1-x)$ and $h(z)$ is doubly positive, then $f(x)$ is enveloped by the linear fractional function*

$$\phi(x) = \frac{1 - \alpha x}{\alpha + (1 - 2\alpha)x}$$

where $\alpha = \frac{3-h_2}{4-h_2} \geq \frac{1}{2}$ and the model $x_{t+1} = f(x_t)$ is globally stable.

Proof. Recasting in terms of $z = 1 - x$ we want to show that $\phi(z) - (1-z)h(z) > 0$ for $z \in (0, 1)$ and $\phi(z) - (1-z)h(z) < 0$ for $z \in (-\frac{1-\alpha}{\alpha}, 0)$ where $\phi(z) = \frac{1+\beta z}{1-(1-\beta)z}$ and $\beta = \frac{\alpha}{1-\alpha}$. Assuming that $h(z)$ has a power series, the function we want to bound can be written as:

$$\begin{array}{cccccc} 1 & + \beta z & & & & \\ -h_0 & -h_1 z & -h_2 z^2 & -h_3 z^3 & -\dots & \\ & +(2-\beta)h_0 z & +(2-\beta)h_1 z^2 & +(2-\beta)h_2 z^3 & +\dots & \\ & & -(1-\beta)h_0 z^2 & -(1-\beta)h_1 z^3 & -\dots & \end{array}$$

By the assumption on h_0 and h_1 , the coefficients of z^0 and z^1 vanish. By choosing $\beta = 3 - h_2$ the coefficient of z^2 vanishes. The succeeding coefficients can be written as

$$(\beta - 1)[h_n - h_{n+1}] + [h_{n+1} - h_{n+2}]$$

with $n \geq 1$. By assumption $\beta = 3 - h_1 \geq 3 - h_1 = 1$. So assuming that $h_n \geq h_{n+1}$ makes all these coefficients nonnegative, and for the power series to converge at least one of these inequalities must be strict, and hence $\phi(z) - (1-z)h(z) > 0$ for $z \in (0, 1)$. We have shown that

the function has the form $z^3p(z)$, so to show that it is *negative* on $(-1/\beta, 0)$, which will follow if $p(z)$ is positive on $(-1/\beta, 0)$ and this will follow if $p_n - \frac{1}{\beta}p_{n+1} \geq 0$ where p_n and p_{n+1} are the n^{th} and $n+1^{\text{st}}$ coefficients of $p(z)$. From above, this is

$$(\beta - 1)[h_n - h_{n+1}] + \frac{1}{\beta}[h_{n+1} - 2h_{n+2} + h_{n+3}] \geq 0$$

which will be nonnegative by the assumptions, and at least one inequality will be positive if the power series converges. \square

While this doubly positive condition will be sufficient for a number of models, it is not sufficient for all the examples because, in particular, β will be less than 1 for some of the models. The following observation will be useful in many cases.

Observation 1 *Let $\phi(x) = A(x)/B(x)$, $f(x) = C(x)/D(x)$ and $G(x) = A(x)D(x) - B(x)C(x)$. If $G(1) = 0$, $G'(1) = 0$, and $G''(x) > 0$ on $(0, 1)$ and $G''(x) < 0$ for $x > 1$, then $\phi(x)$ envelops $f(x)$. (We are implicitly assuming that A, B, C, D are all positive, and all functions are twice continuously differentiable.)*

Proof. Obviously, if $G'(1) = 0$ and $G''(x) > 0$ on $(0, 1)$ then $G'(x) < 0$ on $(0, 1)$. Also, if $G''(x) < 0$ for $x > 1$, $G'(x) < 0$ for $x > 1$. But then $G(x)$ is always decreasing, and since $G(1) = 0$, $G(x) > 0$ for $x < 1$ and $G(x) < 0$ for $x > 1$. Rewriting this result shows that $\phi(x)$ envelops $f(x)$. \square

If convenient we can switch to the variable $z = 1 - x$, and, of course, $G''(x) = G''(z)$. So if $G''(z) = zp(z)$ where $p(z)$ is strictly positive then $\phi(x)$ envelops $f(x)$.

SIMPLE MODELS OF POPULATION GROWTH

In this section we will apply the techniques of the previous section to 7 models from the literature.

Model I

The model $x_{t+1} = x_t e^{r(1-x_t)}$ is widely used (see, for example [May74, Mor50, Ric54]). Our first observation is that $0 < r \leq 2$ is the necessary condition for local stability. It is easy to show that this model with $0 < r < 2$ is enveloped by this model with $r = 2$. As we showed earlier, this model with $r = 2$ is enveloped by $\phi(x) = 2 - x$ and hence local and global stability coincide. It is also easy to check that the doubly positive condition holds for this model. Specifically,

$$h(z) = e^{2z} = 1 + z + \frac{2^2 z^2}{2!} + \frac{2^3 z^3}{3!} + \dots$$

and $h_0 = 1$, and $h_1 = 2$, and

$$h_n - h_{n+1} = \frac{2^n}{(n+1)!} [n+1-2] = \frac{2^n(n-1)}{(n+1)!} \geq 0$$

for $n \geq 1$ and

$$h_n - 2h_{n+1} + h_{n+2} = \frac{2^n}{(n+2)!} [n^2 - n - 2] \geq 0$$

for $n \geq 2$.

Model II

The model $x_{t+1} = x_t[1 + r(1 - x_t)]$ is widely used [Smi68] and is sometimes considered to be a truncation of Model I. As for Model I the necessary condition for local stability is $0 < r \leq 2$, and like Model I it is easy to show that this model with $0 < r < 2$ is enveloped by this model with $r = 2$. Unlike Model I, this model is not enveloped by a straight line. But the doubly positive condition holds. Specifically, $h(z) = 1 + 2z$, so

$$h_n - h_{n+1} = \left\{ \begin{array}{ll} 2 - 0 & n = 1 \\ 0 - 0 & n > 1 \end{array} \right\} \geq 0$$

and

$$h_n - 2h_{n+1} + h_{n+2} = \left\{ \begin{array}{ll} 2 & n = 1 \\ 0 & n > 1 \end{array} \right\} \geq 0.$$

Since $h_2 = 0$, the enveloping function has $\alpha = \frac{3}{4}$ and is

$$\phi(x) = \frac{4 - 3x}{3 - 2x}.$$

In this simple example, it's easy to check that the enveloping condition is equivalent to $(1 - x)^3$ having a single change of sign which occurs at $x = 1$.

Model III

The model $x_{t+1} = x_t[1 - r \ln x_t]$ is attributed to Gompertz and studied by Nobile *et al* [NRS82]. As with the preceding two models $0 < r \leq 2$ is the necessary condition for local stability, the model with $r = 2$ envelops the model with $0 < r < 2$, and the doubly positive condition holds. Specifically,

$$h(z) = 1 - 2 \ln(1 - z) = 1 + 2z + \frac{2z^2}{2} + \cdots + \frac{2z^n}{n} + \cdots$$

and $h_n - h_{n+1} = \frac{2}{n(n+1)} > 0$ for $n \geq 1$ and $h_n - 2h_{n+1} + h_{n+2} = \frac{4}{n(n+1)(n+2)} > 0$ for $n \geq 1$. Since $h_2 = 1$, the enveloping function has $\alpha = 2/3$ and is $\phi(x) = \frac{3-2x}{2-x}$.

Model IV

Model IV is

$$x_{t+1} = x_t \left(\frac{1}{b + cx_t} - d \right).$$

from [Uti57]. This model differs from the previous three in that there are two parameters, b and d , remaining after the carrying capacity has been normalized to 1. The necessary condition for local stability gives

$$\frac{d-1}{(d+1)^2} \leq b < \frac{1}{d+1}.$$

To avoid a pole for $x > 0$, we also assume, $d > 1$. It is easy to check that this model with $b = \frac{d-1}{(d+1)^2}$ envelops this model with larger values of b . With these assumptions

$$f(x) = x \left[\frac{(d+1)^2}{d-1+2x} - d \right]$$

and

$$h(z) = \frac{d+1}{1 - \frac{2}{d+1}z} - d.$$

Since $d > 1$,

$$h(z) = 1 + 2z + \frac{2^2}{d+1}z^2 + \frac{2^3}{(d+1)^2}z^3 + \dots$$

and

$$h_n = \frac{2^n}{(d+1)^{n-1}} \text{ for } n \geq 1.$$

So,

$$h_n - h_{n+1} = \frac{2^n}{(d+1)^n} (d-1) > 0$$

and

$$h_n - 2h_{n+1} + h_{n+2} = \frac{2^n(d-1)^2}{(d+1)^n} > 0.$$

The enveloping function is

$$\phi(x) = \frac{4d - (3d-1)x}{3d-1+2(1-d)x}$$

and has

$$\alpha = \frac{3d-1}{4d} > \frac{1}{2}.$$

We note that $\phi(x)$ has a pole, but $\phi(x)$ goes to zero before the pole, so we can simply ignore the pole. Of course, we only need $\phi(x)$ to bound $f(x)$ on the interval $(0, \frac{4d}{3d-1})$ where $\phi(x)$ is positive.

Model V

Model V has

$$f(x) = \frac{(1 + ae^b)x}{1 + ae^{bx}}$$

and comes from Pennycuick *et al* [PCB68]. This and the following two model are more complicated than the previous models because we have to consider different enveloping functions for different parameter ranges.

For $b \leq 2$, $xe^{b(1-x)}$ envelops $f(x)$ because $e^{b(1-x)} + ae^{bx} \bowtie 1 + ae^b$ since $e^{b(1-x)} \bowtie 1$ for $b > 0$. (Here we are using the notation $g(x) \bowtie h(x)$ to mean $g(x) > h(x)$ for $x \in (0, 1)$ and $g(x) < h(x)$ for $x > 1$ and still in the range of interest.) But $xe^{b(1-x)}$ is just Model I, and as we showed it is enveloped by $2 - x$. So Model V is globally stable for $b \leq 2$. Of course, the inequality still holds for $b > 2$, but since Model I is *not* stable for $b > 2$, the inequality does not help in establishing the stability of Model V.

For this model we assume that $a > 0$ and $b > 0$. The necessary condition for local stability gives $a(b-2)e^b \leq 2$. It is easy to show that this model with larger values of a envelops this model with smaller values of a . Letting $ae^b = \frac{2}{b-2}$ and using $z = 1 - x$ we have

$$f(z) = \frac{b(1-z)}{(b-2) + 2e^{-bz}}.$$

The enveloping linear fractional is

$$\phi(x) = \frac{b - (b-1)x}{(b-1) - (b-2)x}$$

or converting to $z = 1 - x$,

$$\phi(z) = \frac{1 + (b-1)z}{1 + (b-2)z}.$$

Following the technique of the Observation, we have,

$$G(z) = (b-2) + 2e^{-bz} + (b-1)(b-2)z + 2(b-1)ze^{-bz} - b(1-z) - b(b-2)z(1-z).$$

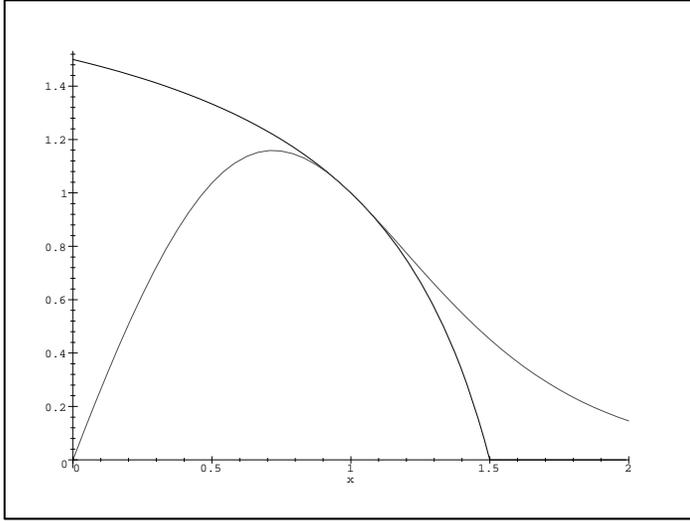


FIGURE 4. Model V with $b=3$, enveloped by the linear fractional $\frac{3-2x}{2-x}$.

It is easy to check that $G(0) = G'(0) = 0$. Finally,

$$G''(z) = z\{2b(b-2)\left(\frac{1-e^{-bz}}{z}\right) + 2(b-1)b^2e^{-bz}\}.$$

Clearly, $\frac{1-e^{-bz}}{z}$ is positive for all $z \neq 0$ and since $b > 2$, the first term in $\{-\}$ brackets is positive. Of course, the second term is also positive. So by the Observation, Model V is enveloped as claimed.

Model VI

Model VI is from Hassel [Has74] and has

$$f(x) = \frac{(1+a)^b x}{(1+ax)^b} \quad \text{with } a > 0, b > 0.$$

There are two cases to consider $0 < b \leq 2$ and $b > 2$. The enveloping function for $b \leq 2$ is $\phi(x) = 1/x$. Cross multiplication shows that we want $(1+ax)^b \asymp (1+a)^b x^2$. Taking b^{th} roots and rearranging shows that we want $1-x+ax(1-x^{\frac{2-b}{b}}) \asymp 0$. Clearly, each of the two terms is positive (nonnegative) below 1 and negative (nonpositive) above 1, and so enveloping is established.

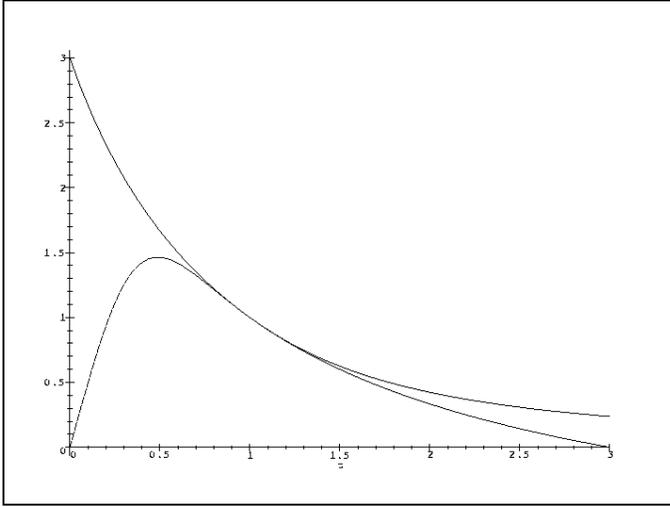


FIGURE 5. Model VII with $c=2.5$ showing envelopment by a linear fractional.

The local stability condition implies that $a(b-2) \leq 2$. It is also easy to show that this model with smaller values of a is enveloped by this model with larger values of a . So if $b > 2$, we can use $a = \frac{2}{b-2}$ or equivalently $b = \frac{2+2a}{2}$ to simplify formulas. Cross multiplication gives

$$G(x) = 2(b-1)(1+ax)^b - (b-2)(1+ax)^b - (b-2)(1+a)^b x - 2(1+a)^b x^2.$$

Simplification and multiplication by $a/2$ gives $G(x) \equiv (2+a)(1+ax)^{b-1} - x(1+ax)^{b-1} - (1+a)^b x$ and

$$G''(x) \equiv (2+a)^2 a(b-2)(1+ax)^{b-3} - a(b-1)(1+ax)^{b-2} - (2+a)(1+ax)^{b-2} - (2+a)a(b-2)x(1+ax)^{b-3}.$$

Dividing by $(1+ax)^{b-3}$ and simplifying gives

$$G''(x) \equiv (2+a)^2 2 - 2(2+a)(1+ax) - 2(2+a)x \equiv 2(2+a)(1+a)(1-x).$$

So $G''(x) \propto 0$ and enveloping is established. (In this argument we use \equiv to indicate that two quantities have the same sign, but not necessarily the same value.)

Model VII

Model VII is due to Maynard Smith [Smi74] and has

$$f(x) = \frac{rx}{1+(r-1)x^c}.$$

This seems to be the hardest to analyze model in our set of examples. For example, this model does not satisfy the Schwarzian derivative condition or Cull's condition **A**. Even for our enveloping analysis, we will need to consider this model as three subcases.

Similar to previous models, local stability implies $r(c-2) \leq c$, and it is easy to show that this model with smaller values of r is enveloped by this model with larger values of r .

We first consider the situation when $c \in (0, 2]$. Here, local stability does not place an upper bound on r . Of course, we assume $r > 1$ for this to be a population model. The enveloping function here is $\phi(x) = 1/x$, that is the linear fractional with $\alpha = 0$. Cross multiplication shows that we need

$$1 + (r-1)x^c - rx^2 \asymp 0$$

for enveloping. Rewriting this gives $1 - x^c + rx^c(1 - x^{2-c}) \asymp 0$. Clearly, $1 - x^c > 0$ and $1 - x^{2-c} \geq 0$ for $1 > x$ and $2 \geq c$, and $1 - x^c < 0$ and $1 - x^{2-c} \leq 0$ for $1 < x$ and $2 \geq c$, so enveloping is established.

For $c > 2$, we use $r = \frac{c}{c-2}$, and show that

$$\phi(x) = \frac{c-1-(c-2)x}{c-2-(c-3)x}$$

is the enveloping function. As before, we calculate

$$\begin{aligned} G(x) &= 2x^c[(c-1)-(c-2)x] + (c-1)(c-2) - 2(c-1)(c-2)x + c(c-3)x^2 \\ G'(x) &= 2x^{c-1}[c(c-1)-(c+1)(c-2)x] - 2(c-1)(c-2) + 2c(c-3)x \\ G''(x) &= 2x^{c-2}[c(c-1)^2 - c(c+1)(c-2)x] + 2c(c-3) \\ &= 2c\{(c-1)^2x^{c-2}[1-x] + (c-3)[1-x^{c-1}]\}. \end{aligned}$$

So for $c \geq 3$, $G''(x) \asymp 0$ and $\phi(x)$ envelops $f(x)$.

We are left with the case when $c \in (2, 3)$.

$$\frac{G''(x)}{2c} = -(c+1)(c-2)x^{c-1} + (c-1)^2x^{c-2} - (c-3)$$

and so, $G''(x)$ has two positive real roots. One of these is, of course, the root at $x = 1$. Now, taking another derivative, $G'''(x)$ is clearly decreasing at $x = 1$, and hence the other root occurs for some $x < 1$. Since $G''(0) < 0$, G'' will start out negative, become positive, and then become negative for all $x > 1$. But now consider $G'(x)$. $G'(0) < 0$ and so while G'' is negative, G' will become more negative, and when G'' becomes positive, G' will increase from a negative value up to 0 at $x = 1$, and then since $G'' < 0$, G' will decrease and stay negative. Hence G which starts positive will decrease through 0 at $x = 1$ and continue decreasing. So, $G''(x) \asymp 0$ and $\phi(x)$ does envelop $f(x)$.

CONCLUSION

As Rosen [Ros85] states an anticipatory system behaves as if it knows the future. Analysts would like to look at a system and predict its future. There are reasonable analysis techniques

for linear systems, but there are few reasonable techniques for nonlinear systems. In this paper, we have shown that by limiting the dimension to one and considering models that have actually been used in biology, we can find some reasonable analytic techniques

Specifically, we showed that one-dimensional difference equations whose right hand side can be enveloped by a linear fractional function are globally stable. Further, for the example biological models, enveloping is possible exactly when the model is locally stable.

This idea of enveloping captures the idea of a curve being *well-behaved*. Try drawing a curve which starts at the origin, rises to a maximum, goes through (1,1) with a slope at least -1 , and then goes to or toward 0. If this curve does not correspond to a globally stable model, your eye can see some odd behavior. Cull [Cul81,Cul88b] has drawings of such curves. On the other hand, if your curve looks well-behaved, you should be able to draw a linear fractional curve that envelops it.

One surprise in our analysis is that the *one-humped* form is **not** essential. A function can have many humps and still be enveloped. So the technique we have developed is actually applicable to a wider variety of models than those we used as examples.

Another indication that biologists have very well-behaved functions in mind is that the examples are *buffered* in that making the functions slightly more complicated still leaves local stability implying global stability. For example, Model II is a second degree polynomial, but even a third degree polynomial would have local stability implying global stability. Singer [Sin78] notes that this follows from the Schwarzian condition. It also follows from our doubly positive theorem. Cull [Cul88b] shows that a slight generalization of Model I also has local stability implies global stability, and he gives examples of generalizations which do **not** have local implies global.

REFERENCES

- Cul81* P. Cull. Global Stability of Population Models. *Bulletin of Mathematical Biology*, 43:47–58, 1981.
- Cul86* P. Cull. Local and Global Stability for Population Models. *Biological Cybernetics*, 54:141–149, 1986.
- Cul88a* P. Cull. Local and Global Stability of Discrete One-dimensional Population Models. In L. M. Ricciardi, editor, *Biomathematics and Related Computational Problems*, pages 271–278. Kluwer, Dordrecht, 1988.
- Cul88b* P. Cull. Stability of Discrete One-dimensional Population Models. *Bulletin of Mathematical Biology*, 50(1):67–75, 1988.
- Dev86* R. Devaney. *An Introduction to Chaotic Dynamical Systems*. Benjamin, Redwood City, 1986.
- FGV79* M.E. Fisher, B.S. Goh, and T.L. Vincent. Some Stability Conditions for Discrete-time Single Species Models. *Bulletin of Mathematical Biology*, 41:861–875, 1979.
- Goh79* B. S. Goh. *Management and Analysis of Biological Populations*. Elsevier, New York, 1979.
- Has74* M.P. Hassel. Density Dependence in Single Species Populations. *Journal of Animal Ecology*, 44:283–296, 1974.
- Hua86* Y.N. Huang. A Counterexample for P. Cull's Theorem. *Kexue Tongbao*, 31:1002–1003, 1986.
- LaS76* J.P. LaSalle. *The Stability of Dynamical Systems*. SIAM, Philadelphia, 1976.

- LY*⁷⁵ T.-Y. Li and J. Yorke. Period Three Implies Chaos. *American Mathematical Monthly*, 82:985–992, 1975.
- May*⁷⁴ R.M. May. Biological Populations with Nonoverlapping Generations: Stable Points, Stable Cycles, and Chaos. *Science*, 186:645–647, 1974.
- May*⁷⁶ R.M. May. Simple Mathematical Models with Very Complicated Dynamics. *Nature*, 261:459–467, 1976.
- Mor*⁵⁰ P.A.P. Moran. Some Remarks on Animal Population Dynamics. *Biometrics*, 6:250–258, 1950.
- NRS*⁸² A. Nobile, L.M. Ricciardi, and L. Sacerdote. On Gompertz Growth Model and Related Difference Equations. *Biological Cybernetics*, 42:221–229, 1982.
- PCB*⁶⁸ C.J. Pennycuik, R.M. Compton, and L. Beckingham. A Computer Model for Simulating the Growth of a Population, or of Two Interacting Populations. *Journal of Theoretical Biology*, 18:316–329, 1968.
- Ric*⁵⁴ W.E. Ricker. Stock and Recruitment. *Journal of the Fisheries Research Board of Canada*, 11:559–623, 1954.
- Ros*⁸³ G. Rosenkranz. On Global Stability of Discrete Population Models. *Mathematical Biosciences*, 64:227–231, 1983.
- Ros*⁸⁵ R. Rosen. *Anticipatory Systems*. Pergamon Press, New York, 1985.
- Sar*⁶⁴ A. Sarkovskii. Coexistence of Cycles of a Continuous Map of a Line to Itself. *Ukr. Mat. Z.*, 16:61–71, 1964.
- Sin*⁷⁸ D. Singer. Stable Orbits and Bifurcation of Maps of the Interval. *SIAM Journal on Applied Mathematics*, 35(2):260–267, Sept 1978.
- Smi*⁶⁸ J.M. Smith. *Mathematical Ideas in Biology*. Cambridge University Press, Cambridge, 1968.
- Smi*⁷⁴ J.M. Smith. *Models in Ecology*. Cambridge University Press, Cambridge, 1974.
- Uti*⁵⁷ S. Utida. Population Fluctuation, an Experimental and Theoretical Approach. *Cold Spring Harbor Symposium on Quantitative Biology*, 22:139–151, 1957.