# STABILITY AND INSTABILITY IN ONE DIMENSIONAL POPULATION MODELS

Paul Cull, Katie Walsh and Jon Wherry

Received January 21, 2008

Abstract. One dimensional difference equations are widely used in population biology. These seemingly simple models can show a variety of behaviors from *stability* to *chaos*. (see Cull, Yorke, May, Feigenbaum) We show how the **enveloping** technique can be used to demonstrate global and semi-global stability. We discuss the issue of whether *local stability implies global stability*. We give some examples of more complicated behavior which can co-exist with local stability. We show that local stability implies global stability even for models slightly more complicated than the usual models. We address the issue of how complicated a model must be to have local without global stability, and we describe our candidates for the simplest such models.

**1 Introduction** Populations wax and wane. To understand these changes in population, we often use simple models. In this paper, we will study difference equation [10] models of population growth.

Often these models have a single equilibrium point and for some values of the parameters this equilibrium is stable. Biological modelers have often checked for stability with respect to small perturbations and then treated the equilibrium as being stable with respect to large perturbations. Remarkably, this logical jump never caused any difficulties. Eventually, a number of mathematical papers [4, 34, 32] showed that for some of the usual population models *local stability implies global stability.* These papers used a variety of methods including Lyapunov functions [23, 18, 19] Schwartzian derivative [34], and some *ad hoc* techniques [34, 1, 2, 4, 3, 5, 32]. But, one uniform technique applicable to all usual population models was lacking. In particular, it was unclear whether the single hump of population models was sufficient to derive global stability from local stability. Finally, Cull and Chaffee [9, 8] were able to show that the usual population models were bounded by linear fractional functions and that this bounding was enough to show global stability from local stability.

One aspect of the above approaches is the assumption that the models were three times continuously differentiable. Huang [22] pointed out that for some of these arguments, the continuously differentiable assumption was essential. It was also unclear whether biological modelers really wanted to make such an assumption about their models. Cull [13] showed that bounding (*enveloping*) by linear fractionals did not depend on differentiability, and, in fact, such enveloping could apply to discontinuous multi-functions.

In contrast to such stability May [25, 26] and others have shown that without local stability, population models can show complicated behavior including *chaos* [24, 14]. But, is more complicated behavior possible for population models when local stability is assumed? We investigate some generalizations of the usual population models and show that YES, more complicated behavior is possible even with local stability. How much more complicated does a population model have to be to allow more complicated behavior? We show that

2000 *Mathematics Subject Classification.* 92B05, 32A11, 39-02.
*Key words and phrases.* Population models, stability, instability, difference equations, dynamics.

our examples are, in a sense, the simplest population models showing more complicated behavior by showing that $3^{rd}$ order polynomial models and $2^{nd}$ order exponential models are enveloped by linear fractionals and thus still have local stability implies global stability.

We also give an example of a piecewise simple population model which has cycles of every period, but computationally behaves as if it were globally stable.

**1.1 Definitions** 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 $\overline{x}$, the equilibrium point, such that

$$\begin{aligned} &f(0) = 0\,, \\ &f(x) > x \quad \text{for } 0 < x < \overline{x}\,, \\ &f(x) = x \quad \text{for } x = \overline{x}\,, \\ &f(x) < x \quad \text{for } x > \overline{x}\,, \end{aligned}$$

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

$$\begin{aligned} &f'(x) > 0 \quad \text{for } 0 \leq x < x_m\,, \\ &f'(x) < 0 \quad \text{for } x > x_m \text{ such that } f(x) > 0. \end{aligned}$$

We will allow the possibility that $f(x) = 0$ for all $x \geq x_\infty$ and therefore, that $f(x)$ is not strictly differentiable at $x_\infty$. 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 $\overline{x}$ then $x_t$ will overshoot and undershoot $\overline{x}$. Possibly this oscillation will be sustained, or possibly $x_t$ will settle down at $\overline{x}$. 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

$$\lim_{t\to\infty} x_t = \overline{x}$$

where $\overline{x}$ 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 $\overline{x}$, if $x_0$ is in this neighborhood, then $x_t$ is in this neighborhood for all $t$, and

$$\lim_{t\to\infty} x_t = \overline{x}.$$

**2 Global Stability** For global stability, a slight modification of a very general theorem of Sarkovskii [33] gives:

**Theorem 1.** *A continuous population model is globally stable iff it has no cycle of period 2. (That is, there is no point except $\overline{x}$ such that $f(f(x)) = x$.)*

This theorem has been noted by Cull[1] and Rosenkranz[32].

We now state Sarkovskii's Theorem which we will need again later.

**Theorem 2 (Sarkovskii's Theorem [33]).** *Order the Natural Numbers as follows:* $3 \prec 5 \prec 7 \prec 9 \prec 11 \prec 13 \prec 15 \prec \ldots \prec 2\cdot 3 \prec 2\cdot 5 \prec 2\cdot 7 \prec 2\cdot 9 \prec \ldots \prec 2\cdot 2\cdot 3 \prec 2\cdot 2\cdot 5 \prec 2\cdot 2\cdot 7 \prec 2\cdot 2\cdot 9 \prec \ldots \prec 2\cdot 2\cdot 2\cdot 3 \prec \ldots \prec 2^5 \prec 2^4 \prec 2^3 \prec 2^2 \prec 2 \prec 1$. *Now let $f$ be a continuous function from the Reals to the Reals and suppose $p \prec q$ in the above ordering. Then if $f$ has a point of least period $p$, then $f$ also has a point of least period $q$.*

## 3 Enveloping

**Theorem 3 (Enveloping Theorem [13]).** *Assume that $f(x)$ maps the open interval $(a, b)$ into itself.* (The map $f(x)$ may be discontinuous and/or multi-valued.) *Further assume that $f(p) = p$ is the unique fixed point of $f$ in this interval, and that there is a continuous self-inverse function $\phi(x)$ which* **envelops** *$f(x)$ on $(a, b)$. Then if $x_0$ is any initial point in this interval and $\langle x_n \rangle$ is any sequence consistent with $x_{t+1} = f(x_t)$ then $\langle x_n \rangle$ converges to $p$.*

We say the $f(x)$ is **enveloped** by $\phi(x)$ on the interval $(a, b)$ containing $p$ when strict bounding holds on the whole interval, that is:

- $\phi(x) > f(x) > x$ for $x \in (a, p)$ ,
- $\phi(x) < f(x) < x$ for $x \in (p, b)$ ,

and to avoid limiting points of $f(x)$ on either $\phi(x)$ or on $x$, except at the fixed point $p$, we assume that for every sequence $\langle x \rangle$,

- if $\lim_{\langle x \rangle \longrightarrow q} f(x) = q$ then $q = p$, and
- if $\lim_{\langle x \rangle \longrightarrow q} f(x) = \phi(q)$ then $q = p$.

**3.1 Enveloping Figure** The following figure shows a globally stable multi-function enveloped by a linear fractional.

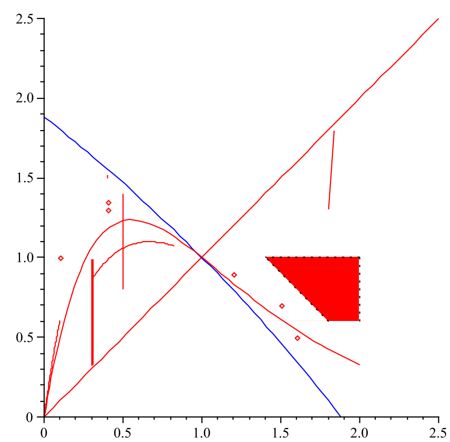



Figure 1: A discontinuous multi-function enveloped by a linear fractional. The linear fractional $\phi(x) = (32 - 17 * x)/(17 - 2 * x)$ is the curve descending from upper left to lower right. The straigh line $y = x$ is the diagonal going from lower left to upper right. The other curves, lines, points, and blobs are parts of the multifunction. Notice that all these pieces are inside the "wedges" formed by the linear fractional and $y = x$. This picture should suggest why we say that the multifunctioned is *enveloped*.

**3.2 Showing Enveloping** From Sarkovskii's Theorem, $f(x)$ is globally stable iff it has has no cycle of period 2. So knowing that one function $f_2(x)$ has no period 2 cycles can be used to show that another function $f_1(x)$ has no period 2 cycles and thus $f_1(x)$ is globally stable.

**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.*

As the Enveloping Theorem states, the enveloping function does not have to be globally stable. Rather, it can be "critical" in the sense of having every point be in a cycle of period 2. For example, the straight line $y = 2 - x$ is a self-inverse function which envelops $x\,e^{2(1-x)}$ and shows that 1 is the globally stable equilibrium point for $g_2(x) = x\,e^{2(1-x)}$. Further since this $g_2(x)$ envelops $x\,e^{\alpha\,(1-x)}$ for each $\alpha$ in $(0, 2)$, we can conclude that 1 is the globally stable equilibrium point for this set of models, $f(x) = x\,e^{\alpha\,(1-x)}$ with $\alpha$ 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

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

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 $\alpha$ 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 2 shows the three different shapes of linear fractional functions.

**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 $n \geq 1$, $\quad h_n \geq h_{n+1}$ ,
4. for all $n \geq 2$, $\quad h_n - 2h_{n+1} + h_{n+2} \geq 0$ .

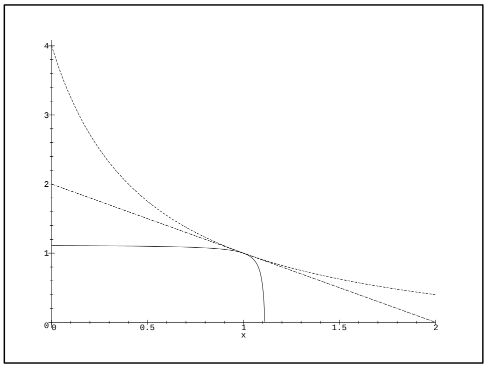



Figure 2: Three linear fractional functions, $\alpha = \frac{1}{4}$, $\alpha = \frac{1}{2}$, $\alpha = .9$.

**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.*

While this doubly positive condition will be sufficient for a number of models, it is not sufficient for all the examples. In particular, models $f_{\mathrm{V}}(x)$, $f_{\mathrm{VI}}(x)$, and $f_{\mathrm{VII}}(x)$, in the following table, are not doubly positive over their whole parametric regions of stability. 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.)*

**4 Summary Table for Some Population Models** The following table summarizes the stability conditions for seven population models. It contains the models, their parametric regions of stability, references to the original sources, and the bounding linear fractionals.

| *Model Number* | *Function* | *Parametric Region for Stability* | *References* | *Enveloping Fractionals* |
|---|---|---|---|---|
| I | $f_{\text{I}}(x) = xe^{r(1-x)}$ | $0 < r \leq 2$ | [18], [25], [27], [31] | $2 - x$ |
| II | $f_{\text{II}}(x) = x(1 + r(1 - x))$ | $0 < r \leq 2$ | [26], [35] | $(4 - 3x)/(3 - 2x)$ |
| III | $f_{\text{III}}(x) = x(1 - r \ln x)$ | $0 < r \leq 2$ | [28] | $(3 - 2x)/(2 - x)$ |
| IV | $f_{\text{IV}}(x) = x\left(\dfrac{1}{b + cx} - d\right)$ | $\frac{d-1}{(d+1)^2} \leq b < \frac{1}{d+1}$ | [37] | $(11 - 8x)/(8 - 5x)$ |
| V | $f_{\text{V}}(x) = \dfrac{(1 + ae^b)x}{1 + ae^{bx}}$ | $0 < a$, $0 < b$,<br>$a(b - 2)e^b \leq 2$ | [29] | $2 - x$ for $b \leq 2$<br>$\frac{b-(b-1)x}{(b-1)-(b-2)x}$ for $b \geq 2$ |
| VI | $f_{\text{VI}}(x) = \dfrac{(1 + a)^b x}{(1 + ax)^b}$ | $0 < a$, $0 < b$,<br>$a(b - 2) \leq 2$ | [20] | $1/x$ for $b \leq 2$<br>$\frac{2(b-1)-(b-2)x}{(b-2)+2x}$ for $b \geq 2$ |
| VII | $f_{\text{VII}}(x) = \dfrac{rx}{1 + (r - 1)x^c}$ | $r(c - 2) \leq c$ | [36] | $1/x$ for $c \leq 2$<br>$\frac{c-1-(c-2)x}{c-2-(c-3)x}$ for $c \geq 2$ |

**5 Instability and Stability in Polynomial Models** In polynomials of degree four it is possible to have local without global stability. This was first introduced in Cull [1], with the example $f(x) = x(x - 3/2)(-2 - (x - 1) - 6(x - 1)^2)$ . The graph of this function is seen in Figure 3.

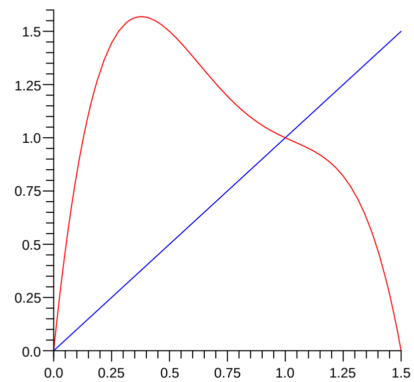



Figure 3: Graph of $f(x) = x(x - 3/2)(-2x - (x - 1) - 6(x - 1)^2)$ plotted with $y = x$. The point where the two curves cross is the equilibrium point $\bar{x}$.

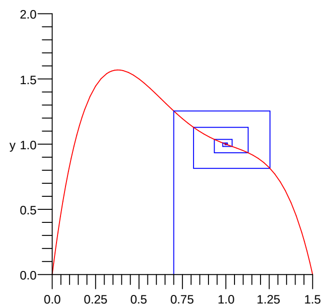
A cobweb plot is an easy way to visualize how a given population model behaves over a series of iterations given an initial population value. In these plots, we draw a vertical line from our initial population value on the x-axis to the point where this value gets mapped (i.e. from $(x_0, 0)$ to $(x_0, f(x_0)))$. Then, we draw a horizontal line to the line $y = x$, i.e. to the point $(f(x_0), f(x_0)$. Then, a vertical line to the function $y = f(x)$, the point $(f(x_0), f(f(x_0)))$. Since $f(x_0) = x_1$, this is the same as drawing a line to the point $(x_1, f(x_1))$. We continue this pattern – alternating vertical and horizontal lines going between $y = x$ and $y = f(x)$.

An example of a cobweb plot using the previously defined $f(x)$ with initial population of .7 is shown in Figure 4a. Here we can see that when $x_0 = .7$, the population ends up at the equilibrium point, $\bar{x} = 1$.

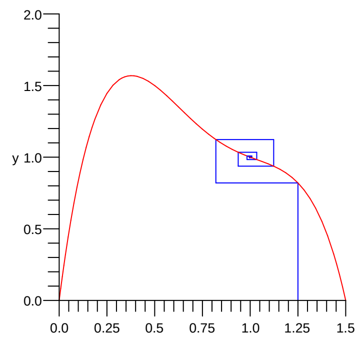
To see where different initial population values tend to after many iterations, we can look at *sequence plots.* In a *sequence plot*, the initial population values are along the $x$-axis, and for each initial $x_0$, the sequence $\langle x_n \rangle$ evaluated for 300 iterations, the first 100 iterates are discarded and the remainder are plotted.

Figure 5a is the sequence plot for our previously defined $f(x)$. From this plot, we can see that there are various intervals where initial population values do not go to 1 after multiple iterations. Since 1 is our equilibrium point, we can see that this is not a globally stable model.

Another way to visualize instabilities in a model is through the application of Sarkovskii's Theorem. According to the theorem, if a function is globally stable, then it has no period-two cycles. In other words, if it has any cycles of any length, then it necessarily has a period two point. To easily check for period two points, we can graph $y = f(f(x))$ and the line $y = x$. Any points of intersection between these two lines are either equilibrium




(a) Cobweb Plot for $f(x)$ with $x_0 = .7$ we see that the cobweb spirals in to the point $(1,1)$, our equilibrium point.




(b) Cobweb plot with $x_0 = 1.25$. When our initial value, $x_0$ is 1.25, the function tends to the equilibrium point after a large number of iterations.

Figure 4: Web plots showing local stability.

points or cycle two points. If there are other points of intersection besides the equilibrium, then the function is not globally stable. Figure 5b shows the graph of $f(f(x))$ for $f(x) = x(x - 3/2)(-2 - (x-1) - 6(x-1)^2)$.

From the graph of $f(f(x))$ we can see that $f(x)$ has two cycles of period two, one that oscillates between approximately .25 and 1.45 and another that oscillates between approximately .625 and 1.35. Since these cycles do not show up in our sequence plot, we can conjecture that they are both unstable cycles, that is, there is no small neighborhood around these points such that the points in this neighborhood map to the cycles.

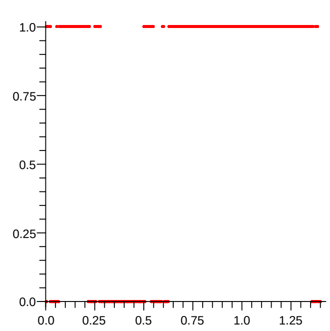
To see where points in the different regions map, we look at the cobweb plots for different initial values. A few cobweb plots for different starting values are shown in Figures 4 and 6.

From Figures 4a and 4b, we can see that 1 is a locally stable point, since values slightly above and slightly below 1 tend towards 1. On the other hand, both period two cycles are unstable, since for values slightly above or below these cycles, the iterates tend towards 1 after many iterations. In Figure 6a and 6b, we can see that the population stays near the two cycle for a short while, but does end up going to 1 after several iterations.

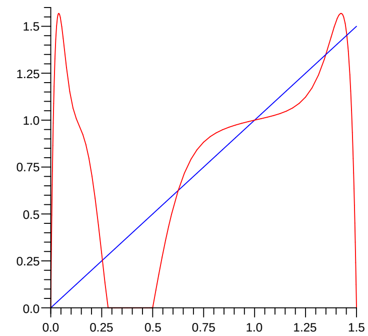
This quartic raises some interesting questions. If a period two oscillation can occur in the quartic, can it arise in lower degree polynomials as well?

**6 Local Stability Implies Global Stability for Polynomials of Degree 3** Let us consider a degree 3 polynomial as a population model. By our assumptions on population models $f(0) = 0$ and $f(1) = 1$ and so the polynomial model has the form

$$f(x) \;=\; x\,\left(1 + b\,(1-x) + c\,(1-x)^2\right).$$




(a) Sequence Plot for $f(x) = x(x-3/2)(-2-(x-1)-6(x-1)^2)$. The $x$-values that map to 1 are points that, after a large number of iterations, tend to the equilibrium point. Since not all $x$-values tend to the equilibrium point, this model is not globally stable.




(b) Graph of $f(f(x))$ against $x$. Since the function $f(f(x))$ crosses the function $x$ at more points than just 0 and $\bar{x}$ this model is not globally stable.

Figure 5: Sequence Plot for $f(x) = x(x - 3/2)(-2 - (x - 1) - 6(x - 1)^2)$. The $x$-values that map to 1 are points that, after a large number of iterations, tend to our equilibrium point. Since not all $x$-values tend to the equilibrium point, this model is not globally stable.

It is easy to see that for any fixed value of $c$, $f_1(x)$ with parameter $b_1$ is enveloped by $f_2(x)$ with with parameter $b_2$ if $b_2 > b_1$. Further, for local stability $b \le 2$. So, to demonstrate global stability for 3$^{\text{rd}}$ polynomial population models, we only need to establish global stability for models of the form:

$$f(x) \;=\; x\left(1 \,+\, 2\,(1-x) \,+\, c\,(1-x)^2\right).$$

We can put a limit on $c$. For a population model $f'(0) \ge 1$, and so we can assume that $c \ge -2$.

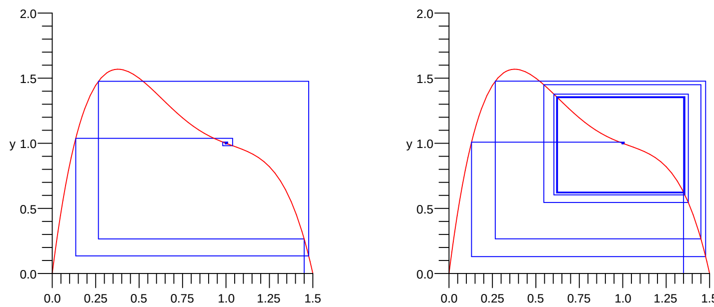
We want a population model to map nonnegative values to nonnegative values, but a third degree polynomial may map some positive values to negative values. Specifically, if $c \le 0$ we can find an $x_\infty$ so that $f(x) < 0$ for $x > x_\infty$. We can make a population model, $\hat{f}(x)$ from such an $f(x)$ by

$$\hat{f}(x) \;=\; \begin{cases} f(x) & 0 \le x \le x_\infty \\ 0 & \qquad x \ge x_\infty \end{cases} .$$

On the other hand, if $c > 0$ then $f(x)$ may have two positive real roots. In particular, for $0 < c < 1$ the first root occurs at

$$1 + \frac{1}{c} - \frac{\sqrt{1-c}}{c}.$$

We can take this root as $x_\infty$ and as above use $\hat{f}(x)$ as our population model. At $c = 1$, these two roots coalesce, but we can still use this double root as the cut-off $x_\infty$.



(a) Cobweb plot with $x_0 = 1.45$. This initial value is near to the period two point detected by plotting $f(f(x))$ against $x$. Notice how it tends to 1. This means that the period two cycle is unstable.

(b) Cobweb plot with $x_0 = 1.35$. This, like our cobweb plot for $x_0 = 1.45$, is a cobweb plot for an initial value close to a detected period two point. Notice how the cobweb forms a dark box, showing that the function maintains a period two cycle for a short while. However, after a large number of iterations, this function tends to 0.

Figure 6: Two cobweb plots showing the period 2 cycles.

For $c > 1$ there is no positive root, but there is a second positive fixed point, that is,

$$f\left(1 + \frac{2}{c}\right) = 1 + \frac{2}{c}.$$

Up to $c = 3$, we can use our usual enveloping. (For the critical value, $c = 3$, $1/x$ serves as the enveloping function.) But right at this parametric point a change in geometry has occurred. For $c < 3$ we the enveloping function goes to 0 at a finite point $x_f$ and we only need to check that $f(x) \geq 0$ for $x > x_f$. So we will have no difficulty in taking a cut-off $x_\infty$ and letting our "population model" have $\hat{f}(x) = 0$ for $x > x_\infty$. But, for $c = 3$, $1/x$ does not go to 0 for any finite value of $x$ and so we cannot make our "population model" become 0 for large values of $x$.

This is telling us that even for $c < 3$, we could have let $\hat{f}(x)$ have any nonnegative value less than $x$ for $x > x_f$, and specifically we could just let $\hat{f}(x) = f(x)$ up to the second positive fixed point. By the geometry of this situation, for any $x_0$ less than this fixed point one of the subsequent iterates $f^{(j)}(x_0)$ will be less than 1, and then the enveloping argument will show that subsequent iterates will converge to 1, and, hence, we will have "global convergence" for

$$x_{t+1} = f(x_t) \qquad \text{for all} \quad x \quad \text{with F.P.} > x > 0$$

where F.P. is the second positive fixed point .

This second fixed point, F.P., is a repellor. Any $x$ slightly less than F.P. is repelled toward smaller values, and any $x$ slightly greater than F.P. is repelled toward larger values. From the argument in the next subsection, we'll see that $f(x)$ is inside the wedges formed by $\phi(x)$ and $x$ on $(0,1)$ and by $x$ and $\phi(x)$ on (1, F.P.). So allowing $f(x)$ to follow a third order polynomial and increase toward its second fixed point will still give "global" stability on (0, F.P.)

So, for $3 \geq c \geq -2$ , we can create resonable ideas for "population models" and as we'll show if one of these has local stability then it is enveloped by a linear fractional and displays global stability.

Let us now consider $4 > c > 3$. For $c > 3$, enveloping becomes a little funny. Our enveloping linear fractional $\phi(x)$ will have a pole in $(0,1)$, and $\phi(x)$ will be negative on $(0, \text{pole})$. So, we cannot expect such a linear fractional to upper bound a positive function. We can save enveloping here by noting that "all the action" occurs on $(x_M, f(x_M))$ rather than on the whole interval $(0, x_\infty)$. So if we can show enveloping on $(x_M, f(x_M))$, we will get global stability on $(0, x_\infty)$ because any point in the wider interval will be eventually mapped by repeated iterations to a point in the interval of envelopment.

Our argument (below) will show that for $c < 4$ we can envelop the 3$^{\text{rd}}$ degree polynomial with a linear fractional. But, when $c = 4$ (or $c > 4$) such enveloping is **not** possible. For $c = 4$, $x_M = 1/2$, the pole of the linear fractional is at 1/2, and

$$f\left(\frac{1}{2}\right) = \frac{3}{2} = \text{F.P.}$$

and so we cannot have "global" stability on (0, F.P.). If $c > 0$, $f(x)$ has a fixed point, F.P. $= 1 + 2/c$. Further $f(1/2) = 1 + c/8$ and $1 + c/8 \geq 1 + 2/c$ if $c^2 \geq 16$. So $f(1/2) =$ F.P. if $c \geq 4$ and the model lacks global stability. For $c > 4$, $x_0 = 1/2$ gives an increasing sequence $x_0, x_1, x_2, x_3, \ldots$ which goes off toward $+\infty$.

Our result is still that *local stability implies global stability* for 3$^{\text{rd}}$ degree polynomial population models. But, we can extend enveloping to include 3$^{\text{rd}}$ degree polynomial "population models" which do not satisfy our definition of population models.

We should mention if $2 \geq c \geq 0$ then $f(x) = x\,h(z)$ has $h(z)$ doubly positive and by Theorem 4, $f(x)$ is globally stable. Here we need a cut-off $x_\infty$ which we can take as the positive root of $f(x)$ for $1 \geq c \geq 0$ or as the fixed point, F.P., for $2 \geq c \geq 1$.

**6.1 Enveloping by a linear fractional** According to our definition, a linear fractional has the form

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

but here we'll find it more convenient to recast these functions by using the variable $z$ where $z = 1 - x$ and the parameter $\beta$ where $\beta = \frac{\alpha}{1-\alpha}$ giving

$$\phi(z) = \frac{1 + \beta z}{1 - (1-\beta)z} = 1 + z + (1-\beta)\,z^2 + \frac{(1-\beta)^2\,z^3}{1 - (1-\beta)z}.$$

We want to envelop a third degree polynomial population model. We can assume that the model has the form

$$\begin{aligned} f(x) &= x\,h(z) = (1 - z)\,h(z) \\ &= (1 - z)\,[1 + 2z + c\,z^2] \\ &= 1 + z + (c-2)\,z^2 - c\,z^3 \end{aligned}$$

To envelop $(1 - x)\,h(z)$ by $\phi(z)$, we take $1 - \beta = (c-2)$, and after eliminating terms, we need to show that

$$\frac{(c-2)^2\,z^3}{1 - (c-2)z} \bowtie -c\,z^3,$$

but dividing by $z^3$ and taking account of the signs, we need

$$\frac{(c-2)^2}{1-(c-2)z} > -c \qquad (**)$$

for all relevant values of $z$. We might mention that (**) is obviously valid for $c = 2$ and for $c = 3$.
For our usual enveloping, we need this inequality for $1 > z > -1/\beta$, but we'll also want to consider some slight modifications of this usual enveloping.)

Since $\frac{(c-2)^2}{1-(c-2)z}$ is decreasing for $c < 2$, we can establish enveloping by checking the inequality $(**)$ at $z = 1$. We want $\frac{(c-2)^2}{1-(c-2)} > -c$. We can cross multiply by $3-c$ because $2 \geq c$, and after subtracting terms, we get the valid inequality $4 > c$.

Since $\frac{(c-2)^2}{1-(c-2)z}$ is increasing for $c > 2$, we can establish enveloping by checking the inequality $(**)$ at $z = -1/\beta = -1/(3-c)$. We want

$$\frac{(c-2)^2}{1+\frac{c-2}{3-c}} = (3-c)\,(c-2)^2 > -c$$

and we establish this inequality by using $\gamma = c-2$ making the inequality

$$(-\gamma + 1)\,\gamma^2 > -(\gamma + 2)$$

$$\text{or} \quad -\gamma^3 + \gamma^2 + \gamma + 2 = -(\gamma - 2)\,(\gamma^2 + \gamma + 1)$$

which is obviously valid for $2 > \gamma \geq 0$, i.e., for $4 > c \geq 2$.

The situation is slightly more complicated for $4 > c > 3$. Here we are dealing with abnormal enveloping because the pole of the linear fractional occurs in the $x$ interval (0, 1). the linear fractional is not even a linear fractional according to our definition because $\alpha = \frac{3-c}{4-c} < 0$.

Instead of enveloping on the whole $x$ range (0, F.P.), we will establish enveloping on the $x$ range (pole, F.P.). This is enough to establish global stabilty on the larger $x$ range as long as the the maximum point $x_M$ for $f(x)$ occurs above the pole.
Since, as we mentioned above, $\frac{(c-2)^2}{1-(c-2)z}$ is increasing for $c > 2$, we can establishing enveloping by checking the inequality $(**)$ at the most negative value of $z$ which is $1 - \text{F.P.} = -2/c$, but there's nothing to check because (**) is obviously valid for negative $z$'s since with $c > 2$ the LHS is positive and the RHS is negative.
We verify that $x_M$ occurs after the pole, $\frac{3-c}{2-c}$, by showing that $f'(\frac{3-c}{2-c})$ is positive. In mixed $x, z$ notation,

$$f'(x) = [1 + 2z + cz^2] - x\,[2 + 2cz]\,.$$

Substituting $x = \frac{3-c}{2-c}$ and $z = \frac{1}{c-2}$ gives, after some simplification,

$$f'(\text{pole}) = \frac{2}{c-2} > 0\,.$$

We summarize these results in the following theorem.

**Theorem 5.** *Any locally stable population model of the form*

$$f(x) \;=\; x\,[\,b\,(1-x) \;+\; c\,(1-x)^2\,]$$

*can be enveloped by a linear fractional with* $\alpha = \frac{3-c}{4-c}$*, and hence will be globally stable.*
*For* $1 \geq c \geq -2$*, this is normal enveloping on the range from* $x = 0$ *to the positive root of* $f(x)$*.*
*For* $3 \geq c > 1$*, this is normal enveloping on the range from* $x = 0$ *to the positive fixed point of* $f(x)$*.*
*For* $4 > c > 3$*, this is enveloping on the restricted range of* $x$ *from the pole of* $\phi(x)$ *to the positive fixed point of* $f(x)$*.*

**7 Exponential Function Population Models** It is also possible to have an exponential function that displays local but not global stability. One such function, which we will examine next, is the exponential function $f(x) = e^{-q(x)}$ where

$$q(x) = 1.9(x-1) - (7.6 - 8\ln 3)(x-1)^3.$$

The graph of the function is in Figure 7

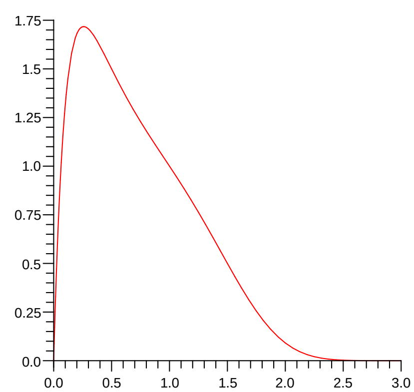
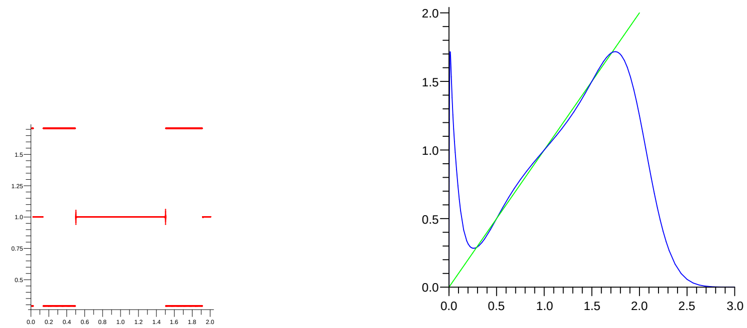



Figure 7: Plot of $f(x) = e^{-q(x)}$ where $q(x) = 1.9(x-1) - (7.6 - 8\ln 3)(x-1)^3$.

Since this function does not go to zero, as the last one did, we will not have the same type of instabilities as the previous function. This function, however, is also not globally stable. We can easily see this from looking at a sequence plot.

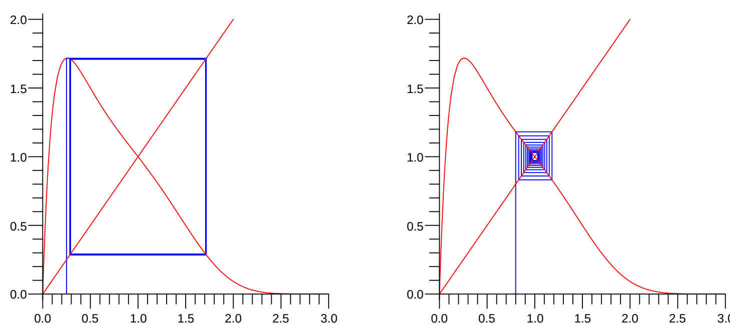
In Figure 8, we see that not only is this graph not globally stable (i.e. not every initial population value tends to 1), but also that there is a stable period two. If we look at the plot of $f(f(x))$ and $y = x$, we can see that in fact this function has two period two cycles. One of these cycles is stable, while the other is not. In Figures 9 and 10, we can see where different initial population values tend to by looking at the different cobweb plots.




(a) Sequence plot of $f(x)$. Notice how in addition to the places that tend to 1 after several iterations, there are initial values that tend to two values after several iterations. These are period two cycles.

(b) Plot of $f(f(x))$ against $x$. Since the graph of $f(f(x))$ crosses the line $y = x$ in places other than 0 and the equilibrium point, $f(x)$ is not globally stable.

Figure 8: Two plots showing that period 2 cycles exist.




(a) Cobweb Plot for $f(x)$ with $x_0 = .25$. This initial value was in the region of the sequence plot that mapped to two values. Notice how it gives a period two cycle.

(b) Cobweb Plot for $f(x)$ with $x_0 = .80$. This initial value was in the region of the sequence that mapped to 1. Notice how it spirals in to one equilibrium point.

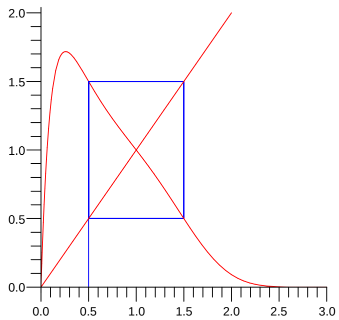
Figure 9: Two plots showing a period 2 cycle and a stable equilibrium.

**8 Local Stability implies Global Stability for $f(x) = xe^{-q(x)}$** Here, we will show that local stability implies global stability for population models of the form

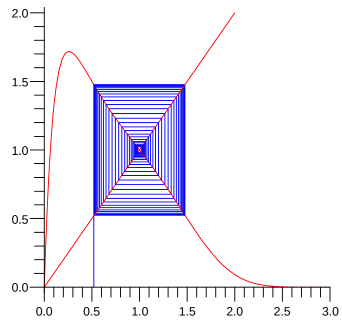
$$f(x) = x\, e^{q(x)} \;=\; x\, e^{\text{degree 2 polynomial}}.$$

It will be convenient to write $f(x)$ in the form:

$$f(x) = x\, e^{a\,+\,b\,z\,+\,c\,z^2} \qquad \text{where} \quad z \,=\, 1 - x.$$




(a) Cobweb Plot for $f(x)$ with $x_0 = .50$. This is an initial value for a value slightly before the part of the sequence plot where it goes from tending to two points to tending toward one point.




(b) Cobweb Plot for $f(x)$ with $x_0 = .52$. This initial value is slightly after the part of the sequence plot where it changes from tending toward two points to tending toward one. The above cobweb plot shows that it tends towards the equilibrium, but the darkness of the plot indicates it takes a long time to converge.

Figure 10: Two plots showing the approach to and divergence away from the unstable period two cycle toward the stable equilibrium.

We now use the conditions on population modes to restrict the values of the three parameters $a$, $b$, $c$. Since $f(1) = 1$, we are forced to take $a = 0$. For a fixed value of $c$, if $b > B$ then $f_b(x)$ envelops $f_B(x)$. Also, $f'(1) = 1 - b$, and so for local stability $2 \geq b$. Finally, if $c > 0$ then $f(x)$ would have a second fixed point at some $x$ greater than 1. These considerations allow us to limit our arguments to $f(x)$'s of the form

$$f(x) = x\,e^{2\,z + c\,z^2} \qquad \text{with} \quad c \leq 0.$$

Besides its fixed point at $x = 1$, $f(x)$ has a fixed point at $1 + 2/c$. For positive $c$, this point will be above $x = 1$ and we have to dismiss this possibility for a population model. For negative $c$, this point will be below $x = 0$ if $c$ is between 0 and $-2$, but if $c < -2$ this fixed point appears in the interval $(0, 1)$. So we only have to consider $f(x)$'s of the form

$$f(x) = x\,e^{2\,z + c\,z^2} \qquad \text{with} \quad -2 \leq c \leq 0.$$

We demonstrate the global stability of such $f(x)$'s by showing that they are enveloped by linear fractionals. Instead of using $x$, we work with functions of $z$ where $z = 1 - x$. Our linear fraction $\phi(z)$ is

$$\phi(z) \;=\; \frac{1 + \beta\,z}{1 - (1 - \beta)\,z} \qquad \text{where} \quad \beta \;=\; \frac{\alpha}{1 - \alpha}.$$

We choose $\beta = c - 1$, so that the linear fractional matches $f(x)$ through $2^{\text{nd}}$ order terms. Then we want to show that

$$\frac{1 + (1 - c)\,z}{1 - c\,z} \bowtie (1 - z)\,h(z) \;=\; (1 - z)\,e^{2\,z \,+\, c\,z^2}.$$

Taking logarithms and rearranging, we want to show that

$$L(x) \;\bowtie\; 0$$

where

$$L(x) \;=\; \ln[1+(1-c)z] \,-\, \ln[1-cz] \,-\, \ln[1-z] \,-\, 2z \,-\, cz^2 \,.$$

Since $L(1) \;=\; 0$, we can establish the inequality by showing that $L'(x) \;\leq\; 0$ throughout the interval of interest. In $x$, this interval is the positive reals from 0 up to the zero of the linear fractional. In $z$, this interval is $(\,-\frac{1}{(1-c)},\, 1\,)$.

Taking the derivative $L'(x)$ with respect to $x$, we have

$$L'(x) \;=\; -\frac{1-c}{1+(1-c)z} - \frac{c}{(1-cz)} - \frac{1}{(1-z)} \;+\; 2(\,1+cz\,).$$

Adding the first two terms gives

$$L'(x) \;=\; \frac{-1}{[1-cz]\,[1+(1-c)z]} - \frac{1}{(1-z)} \;+\; 2(\,1+cz\,).$$

Multiplying by $[1-cz]$ leaves

$$[1-cz]\,L'(x) \;=\; \frac{-1}{[1+(1-c)z]} - \frac{[1-cz]}{(1-z)} \;+\; 2(\,1\;-\;c^2\,z^2\,).$$

Adding 1 to each of the first two terms and subtracting 2 from the last term gives

$$\begin{aligned} 1 - \frac{-1}{[1+(1-c)z]} &+ 1 - \frac{[1-cz]}{(1-z)} - 2\,c^2\,z^2 \\ &= (1-c)z\left[\frac{1}{[1+(1-c)z]} - \frac{1}{(1-z)}\right] - c^2\,z^2 \\ &= \frac{-(2-c)(1-c)\,z^2}{(1-z)\,[1+(1-c)z]} - 2\,c^2\,z^2 \end{aligned}$$

This quantity is clearly less than 0 (except for $z=0$) on the whole interval of interest.

We summarize these results in the following theorem.

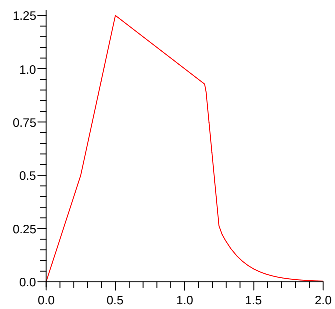
**Theorem 6.** *Any locally stable population model of the form*

$$f(x) = x\,e^{\,b\,z\,+\,c\,z^2}$$

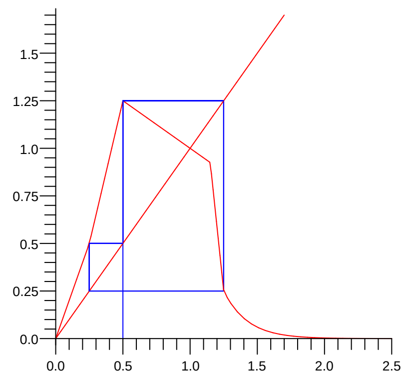
*can be enveloped by a linear fractional with* $\alpha = \frac{1-c}{2-c}$ *and hence will be globally stable.*

**9 Piecewise Simple Model With All Periods** From the previous sections, the question arose as to how complicated a model has to be to show local stability but not global stability. Here, we present a piecewise simple function displaying a period three cycle. From Sarkovskii's Theorem [33], a continuous function with a period three cycle has cycles of every other integer length. Here, we look at creating a piecewise population model that has a cycle of period three and then see where the periods of other lengths appear. Our function, which is shown in Figure 11a, is

$$g(x) = \begin{cases} 2x & \text{if } 0 < x \leq .25, \\ 3x - .25 & \text{if } .25 < x \leq .5, \\ -.5\,x \,+\, 1.5 & \text{if } .75 < x \leq 1.15, \\ -6.75x + 8.6875 & \text{if } 1.15 < x \leq 1.25, \\ e^{-4\ln(.25)(1-x)} & \text{if } 1.25 \leq x. \end{cases} \qquad (1)$$




(a) Plot of the piecewise population model function with period 3.




(b) Cobweb plot for $g(x)$. When the initial value is $x_0 = .5$, the function has a period three cycle through the three points where the cobweb meets the graph of $g(x)$.

Figure 11: A population model with a period 3 cycle.

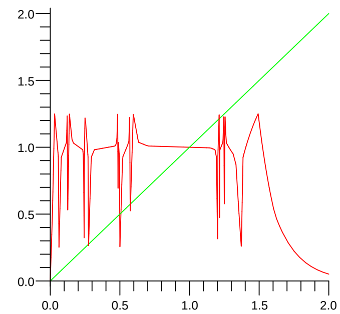
This function was designed so that $g(.5) = 1.25$, $g(1.25) = .25$ and, $g(.25) = .5$. Notice that the function consists of five pieces. The first four segments are straight lines. The fifth segment is an exponential "tail". This design has the properties of a population model. It starts at 0, rises to a maximum, falls to the equilibrium, and tails off to 0 for large vales of $x$. Of course, there is only one positive equilibrium which occurs at $x = 1$. Further, by design, this equilibrium is locally stable because the slope, $f'(1) = -.5$ is less steep than $-1$.

The function has a period three cycle, which can be through the three points where the cobweb meets the graph of $g(x)$ in Figure 11b.

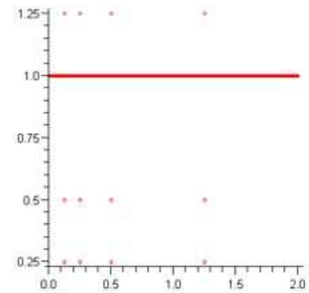
We can look for other cycles by plotting $y = x$ and $g(g(g(...g(x)...)))$ where the number of $g$'s is equal to the length of the cycle. For example, if we wanted to find a five cycle, we would plot $y = x$ and $g(g(g(g(g(x))))))$. This plot in Figure 12a indicates that there are two cycles of period 5..

In spite of the fact that $g(x)$ has cycles of every period, these cycles almost never show up. Figure 12b shows a sequence plot, i.e. the values of $g^{(K)}(x)$ for large values of $K$ when the initial point is $x$. Notice that for almost all initial points, the only value that shows up after a large number of iterations is 1. There are four exceptional points which eventually map to the period 3 cycle. Three of these four are actually on the period 3 cycle.

**10 Conclusion** Nonlinear models are are often difficult or impossible to analyze. [12] Local linearity gives local results, but more global results require addressing the nonlinearity. A central question is when does local stability imply global stability. As we have pointed out, biological modelers have been correct in their jump from local to global stability. We want to know why this extrapolation was valid. We have attempted to answer this question by saying that local implies global for *simple* models. But, this forces the question: What does "simple" mean? We provided a reasonable geometric answer – a function is "simple" if it can be bounded by a linear fractional function. We showed that seven standard pop-




(a) Plot of $y = g(g(g(g(g(x)))))$. Since there are points where the graph crosses the line $y = x$, there are cycles with period 5.




(b) A sequence plot showing that for most initial points, the iterates converge to 1. The period 3 cycle shows up for a few initial points.

Figure 12: Iterations of $g(x)$ showing that cycles and stability both occur.

ulation models can be bounded by linear fractionals. We also showed that enveloping by a linear fractional is more general than these usual models in that the specific single-hump form is not necessary for enveloping. A reasonable conjecture is that modelers may have tried to draw single-hump functions with not too steep a negative slope. As long as one does this as a "smooth" drawing one is almost certain to produce a curve that can be enveloped by a linear fractional. (Try it!)

From the examples in the Table, the standard population models, also, have simple formulas. Can we say anything about how simple a formula must be to have local stability implies global stability? For polynomials, we showed that there is a $4^{\text{th}}$ degree polynomial population model which has local stability without global stability. On the other hand, we proved that every $3^{\text{rd}}$ degree polynomial population model (and some non population models) are enveloped by linear fractionals and so have local stability implies global stability.

For exponential functions, we displayed a population model which has a $3^{\text{rd}}$ degree polynomial in the exponent and is locally but not globally stable. On the other hand, we proved that all population models with which have a have a polynomial of degree at most 2 in the exponential are enveloped by linear fractionals and thus have local stability implies global stability.

What sort of behavior is possible when a population model is not globally stable? We included three examples which show some of the possibilities. As we showed, the $4^{\text{th}}$ degree polynomial population model example has two period 2 cycles and the possibility of crashing to zero. Our computational checks showed that the period 2 cycles are unstable, and that a significant fraction of the initial conditions would cause the population to crash to zero.

For the $3^{\text{rd}}$ degree exponential model, there are again two period 2 cycles, but this time, one cycle is stable and one cycle is unstable. Computer runs showed that a significant fraction of the initial conditions led to this stable period 2 cycle.

Finally, we looked at a piecewise simple model with a period 3 cycle and hence cycles of every period. We demonstrated that some of these periods, e.g. period 5, exist. But, somewhat strangely, this model behaved as if it were almost globally stable, that is, except for four points, all initial conditions gave convergence to the equilibrium.

Our main conclusion, then, is that "simple" population models obey *local stability implies global stability*, and that "simple" includes the usual population models and some slight generalizations. When we were able to quantify the change from "simple" to "complicated", we found that this change required an increase of at least 2 in the the degree of a polynomial appearing in the formula for the model.

## References


[1] P. Cull. Global Stability of Population Models. *Bulletin of Mathematical Biology*, 43:47–58, 1981.

[2] P. Cull. Local and Global Stability for Population Models. *Biological Cybernetics*, 54:141–149, 1986.

[3] P. Cull. Local and Global Stability of Discrete One-dimensional Population Models. In Ricciardi [30], pages 271–278.

[4] P. Cull. Stability of Discrete One-dimensional Population Models. *Bulletin of Mathematical Biology*, 50(1):67–75, 1988.

[5] P. Cull. Linear Fractionals - Simple Models with Chaotic-like Behavior. In Dubois [16], pages 170–181.

[6] P. Cull. Convergence of iterations. In R. Moreno-Diaz et al, editor, *EUROCAST 2005. LNCS 3643*, pages 457–466. Springer-Verlag, Berlin Heidelberg, 2005.

[7] P. Cull. Enveloping Implies Global Stability. In L. Allen B., Aulbach, S. Elaydi, and R. Sacker, editors, *Difference Equations and Discrete Dynamical Systems*, pages 170–181. World Scientific, Hackensack, NJ, 2005.

[8] P. Cull and J. Chaffee. Stability in discrete population models. In D. M. Dubois, editor, *Computing Anticipatory Systems: CASYS'99*, pages 263–275. Conference Proceedings 517, American Institute of Physics, Woodbury, NY, 2000.

[9] P. Cull and J. Chaffee. Stability in simple population models. In R. Trappl, editor, *Cybernetics and Systems 2000*, pages 289–294. Austrian Society for Cybernetics Studies, 2000.

[10] P. Cull, M. Flahive, and R. Robson. *Difference Equations: from Rabbits to Chaos*. Springer, New York, 2005.

[11] Paul Cull. Stability in one-dimensional models. *Scientiae Mathematicae Japonicae*, 58:349–357, 2003.

[12] Paul Cull. Difference Equations as Biological Models. *Scientiae Mathematicae Japonicae*, 64:217– 233, 2006.

[13] Paul Cull. Population Models: Stability in One Dimension. *Bulletin of Mathematical Biology*, 69(3):989–1017, April 2007.

[14] R. Devaney. *An Introduction to Chaotic Dynamical Systems*. Benjamin, Redwood City, 1986.

[15] D. Dubois. Computing Anticipatory Systems with Incursion and Hyperincursion. In D. M. Dubois, editor, *Computing Anticipatory Systems:CASYS'97 - First International Conference, Conference Proceedings 437*, pages 3–29. American Institue of Physics, Woodbury, N.Y., 1998.

[16] D. M. Dubois, editor. *Computing Anticipatory Systems:CASYS 2001 - Fifth International Conference, Conference Proceedings 627*. American Institue of Physics, Woodbury, N.Y., 2002.

[17] M. J. Feigenbaum. Quantitative Universality for a Class of Non-Linear Transformations. *J. Stat. Phys.*, 19:25–52, 1978.

[18] 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.

[19] B. S. Goh. *Management and Analysis of Biological Populations*. Elsevier, New York, 1979.

[20] M.P. Hassel. Density Dependence in Single Species Populations. *Journal of Animal Ecology*, 44:283–296, 1974.

[21] N. Heinschel. Sufficient Conditions for Global Stability in Population Models. *Oregon State University REU Proceedings*, pages 51–67, 1994.

[22] Y.N. Huang. A Counterexample for P. Cull's Theorem. *Kexue Tongbao*, 31:1002–1003, 1986.

[23] J.P. LaSalle. *The Stability of Dynamical Systems*. SIAM, Philadelphia, 1976.

[24] T-Y. Li and J. Yorke. Period Three Implies Chaos. *American Mathematical Monthly*, 82:985–992, 1975.

[25] R.M. May. Biological Populations with Nonoverlapping Generations: Stable Points, Stable Cycles, and Chaos. *Science*, 186:645–647, 1974.

[26] R.M. May. Simple Mathematical Models with Very Complicated Dynamics. *Nature*, 261:459–467, 1976.

[27] P.A.P. Moran. Some Remarks on Animal Population Dynamics. *Biometrics*, 6:250–258, 1950.

[28] A. Nobile, L.M. Ricciardi, and L. Sacerdote. On Gompertz Growth Model and Related Difference Equations. *Biological Cybernetics*, 42:221–229, 1982.

[29] C.J. Pennycuick, 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.

[30] L. M. Ricciardi, editor. *Biomathematics and Related Computational Problems*. Kluwer, Dordrecht, 1988.

[31] W.E. Ricker. Stock and Recruitment. *Journal of the Fisheries Research Board of Canada*, 11:559–623, 1954.

[32] G. Rosenkranz. On Global Stability of Discrete Population Models. *Mathematical Biosciences*, 64:227–231, 1983.

[33] A. Sarkovskii. Coexistence of Cycles of a Continuous Map of a Line to Itself. *Ukr. Mat. Z.*, 16:61–71, 1964.

[34] D. Singer. Stable Orbits and Bifurcation of Maps of the Interval. *SIAM Journal on Applied Mathematics*, 35(2):260–267, Sept 1978.

[35] J.M. Smith. *Mathematical Ideas in Biology*. Cambridge University Press, Cambridge, 1968.

[36] J.M. Smith. *Models in Ecology*. Cambridge University Press, Cambridge, 1974.

[37] S. Utida. Population Fluctuation, an Experimental and Theoretical Approach. *Cold Spring Harbor Symposium on Quantitative Biology*, 22:139–151, 1957.

*Paul Cull*
Computer Science Dept., Oregon State University
Corvallis, OR 97331 USA
E-mail: pc@cs.orst.edu

*Katie Walsh*
Mathematics Dept., George Washington University
Washington, DC 20052 USA
E-mail: kwalsh3@gmail.com

*Jon Wherry*
Mathematics Dept., Oregon State University
Corvallis, OR 97331 USA
E-mail: wherryj@onid.orst.edu