Biol. Cybern. 54, 141–149 (1986)

Biological Cybernetics

Local and Global Stability for Population Models

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Abstract. In general, local stability does not imply global stability. We show that this is true even if one only considers population models.

We show that a population model is globally stable if and only if it has no cycle of period 2. We also derive easy to test sufficient conditions for global stability. We demonstrate that these sufficient conditions are useful by showing that for a number of population models from the literature, local and global stability coincide.

We suggest that the models from the literature are in some sense "simple", and that this simplicity causes local and global stability to coincide.

1 Introduction

Does local stability imply global stability for population models? We will show that the answer is no.

Actually, the issue of local versus global stability for population models is not a clear-cut case of yes and no. The issue only becomes clear-cut when there is an exact definition of population model. We give a definition of population model, and display population models which are locally but not globally stable.

This definition may be rather broad because when we consider specific models from the literature, we find that local stability and global stability coincide. The models from the literature all obey our definition of population model, but in addition these models are in some sense simple. If one could define simple population model, then it might be possible to prove that local and global stability coincide for simple population models. We suggest that defining simple population model may be difficult because the actual models from the literature have different geometric properties, and because we need different methods to prove global stability for geometrically different models.

Since local and global stability do not coincide for population models, we have to investigate conditions for global stability of population models. We will show that a population model is globally stable if and only if the model has no cycles of period 2. Unfortunately, this necessary and sufficient condition may not be easy to test for many specific models. We address this difficulty by deriving some sufficient conditions which are easier to test. Then we show how these sufficient conditions can be used to prove the equivalence of local and global stability for various models from the literature. We include in our demonstration the models used by Nobile et al. (1982). Some of the results of this paper have appeared in Cull (1981).

1.1 Definitions

We will assume that a *population model* has the form

$$X_{t+1}=f(X_t)$$

where f is a continuous function with $f(0)=0$, and there is a unique positive equilibrium point $\bar{X}$ such that

$$f(\bar{X})=\bar{X}, \quad \text{and}$$
$$f(X)>X \quad \text{for} \quad 0<X<\bar{X} \quad \text{and}$$
$$f(X)<X \quad \text{for} \quad \bar{X}<X$$

and such that if $f(X)$ has a maximum X_M in $(0, \bar{X})$ then $f(X)$ is monotonically decreasing for all $X>X_M$ such that $f(X)>0$.

Our definition is similar to that of Nobile et al. (1982) but we do not require $f(X)$ to be 0 for large enough X. We allow population models which have f positive for all positive X. This is really a superficial distinction because the interval $[0, \infty)$ could be rescaled to $[0, 1)$, and then the rescaled population model would be a population model in the sense of Nobile et al. We prefer our form because many of the usual models are given in the literature as being defined on $[0, \infty)$, and we prefer to keep them in their traditional form.

The terms local and global stability cited in the population biology literature are at some variance with the use of the same terms in the mathematical literature. For example, as the terms are used in the mathematical literature, it is possible for a model to be globally stable and fail to be locally stable if the function f is not continuous.

We will use definitions of local and global stability which seem more appropriate in the context of our definition of population model. A population model is *globally stable* iff for all X_0 such that $f(X_0)>0$ we have $\lim_{t\to\infty} X_t=\bar{X}$. A population model is *locally stable* iff there is some small enough neighborhood of $\bar{X}$ such that for all X_0 in this neighborhood, X_t is in this neighborhood and $\lim_{t\to\infty} X_t=\bar{X}$. Using these definitions and our assumptions about population models, global stability implies local stability since we can take as our neighborhood for local stability the whole region in which $f(X)>0$.

When the function $f(X)$ is differentiable in some neighborhood of $\bar{X}$, the necessary condition for local stability is that $-1\leqq f'(\bar{X})\leqq 1$. The condition that $-1<f'(\bar{X})<1$ is a sufficient condition for local stability. Nonlinear terms must be considered to decide local stability when $|f'(\bar{X})|=1$. For the models from the literature we will consider, we will find local (and global) stability when $f'(\bar{X})=-1$, but when $f'(\bar{X})=1$ we will not find local stability because the models degenerate to $f(X)\equiv X$, which does not converge to $\bar{X}$ except when X is already $\bar{X}$. We should note that $f(X)\equiv X$ is *not* a population model according to our definition.

1.2 Some Pictorial Examples

Let us look at some figures and see some pictorial examples where local but not global stability occurs. In Fig. 1, we have a picture of $f(X)$ for a locally and globally stable population model. It is easy to check that the definition of population model is satisfied. To convince yourself that this model is globally stable, pick any X in $[X_M, \bar{X}]$, then go up to the curve, over to the line, down to the curve, and back over to the line. You will find that you are closer to $\bar{X}$ than you were when you started. If you pick any point outside this interval and iterate from there, you will eventually get to a point in $[X_M, \bar{X}]$ and hence you will always converge toward $\bar{X}$.

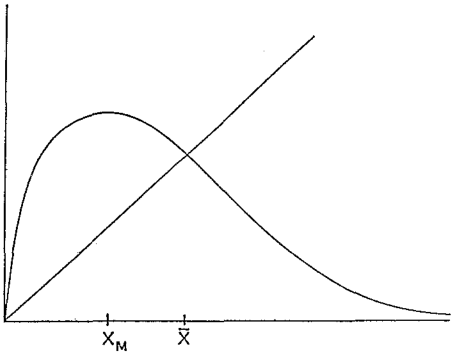

Fig. 1. A population model which is both locally and globally stable

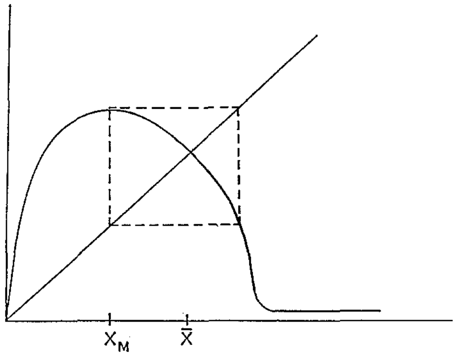

Fig. 2. A population model which is locally but not globally stable because it falls off too quickly

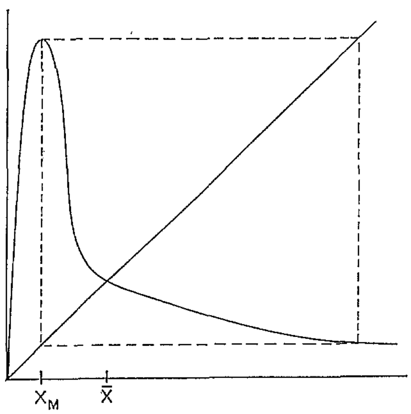

Fig. 3. A population model which is locally but not globally stable because the peak is too high

In Fig. 2, we have another population model. This model is locally stable since $-1<f'(\bar{X})<0$. One can choose any X near $\bar{X}$ and iterate and approach nearer and nearer to $\bar{X}$. This model is not globally stable because there is a cycle of period 2. We may notice that above the equilibrium point this curve drops very quickly toward 0. We have given the curve a rather sharp corner so that it does not actually reach 0. This example shows one way in which a locally stable model can fail to be globally stable: the curve can fall off toward 0 very quickly.

Figure 3 gives another example of a population model which is locally but not globally stable. A cycle of period 2 appears in the figure. There is also another cycle of period 2 which is not drawn. This model differs from the model in Fig. 2 because there is no rapid fall off toward 0. In this model the lack of global stability is due to the peak of the curve being very high.

2 Conditions for Global Stability

The examples in the last section demonstrate that local and global stability do not coincide for population models, but the examples do give us some clues about what extra conditions we might try to add to get global stability. First, notice that when local stability failed there was a cycle of period 2. We will demonstrate that this is always the case for population models. Conversely, we can assure global stability if we can show that a model has no cycles of period 2. Unfortunately, this condition may be difficult to test so we may want to consider some easier to test conditions. Second, notice that in the examples global stability failed because the curve dropped off too quickly or the peak was too high. This suggests that we may be able to impose conditions to prevent these behaviors and thus assure global stability. Third, we recall that local stability depends on the first derivative of the curve, so perhaps we can force global stability by some conditions on the second and higher derivatives of the curve.

We will start investigating the conditions for global stability by giving the necessary and sufficient condition for global stability of population models, which is the absence of cycles of period 2. We should remark that this condition really depends on our definition of population model. There are difference equations with a single equilibrium point which are not globally stable, but have no cycles of period 2. Such difference equations do not satisfy our definition of population model.

Theorem 1. *A population model is globally stable iff it has no cycles of period 2.*

Proof. Clearly a cycle of period 2 would mean that the model is not globally stable since for some initial conditions the model would oscillate around the cycle and never approach the equilibrium.

If there is no cycle of period 2, then $f(f(X))>X$ on $(0,\bar{X})$ because: either $f(X)<\bar{X}$ on this interval and then $f(f(X))>X$ by the definition of population model; or there is some $\hat{X}<\bar{X}$ so that $f(\hat{X})=\bar{X}$ and hence $f(f(\hat{X}))=f(\bar{X})=\bar{X}>\hat{X}$, but no cycle of period 2 implies $f(f(X))-X$ has only one sign $(0,\bar{X})$ and we have a point where $f(f(X))-X$ is positive, so $f(f(X))>X$ throughout the whole interval.

Now $f(f(X))>X$ on $(0,\bar{X})$ implies convergence to $\bar{X}$ for all initial X in $(0,\bar{X})$. If $\bar{X}\geqq f(X)>X$ for all X in $(0,\bar{X})$, then X_t monotonically increases toward $\bar{X}$. Otherwise, if $f(X)>\bar{X}$, then since we have $f(Y)<\bar{X}$ for all $Y>\bar{X}$ from our definition of population model, we have $\bar{X}>f(f(X))>X$ and hence in two steps we are closer to the equilibrium. This gives convergence for all X such that $f(X)>\bar{X}$. For other X in $(0,\bar{X})$, we have strict monotonic increase of X_t until an X_t such that $f(X_t)>\bar{X}$ is reached, and then we have convergence by the previous argument.

Finally, for $X>\bar{X}$ such that $f(X)>0$, we have: either $X_t>\bar{X}$ for all t and thus a monotonic decreasing approach to $\bar{X}$; or $0<X_t<\bar{X}$ for some t, and thus convergence from the above convergence for X in $(0,\bar{X})$. □

Corollary. *A population model is globally stable iff either* (a) *there is no maximum of $f(X)$ in $(0,\bar{X})$; or* (b) *there is a maximum of $f(X)$ at X_M in $(0,\bar{X})$ and $f(f(X))>X$ for all X in $[X_M,\bar{X})$.*

Part (b) of the corollary points out that we only have to worry about convergence in the interval $[X_M,\bar{X}]$ because, starting from any other point, we will eventually be in this interval. The corollary also tells us that there are really only two ways a globally stable population model can behave. In case (a), if the population is initially below the equilibrium, it will monotonically increase toward the equilibrium. If the population is initially above the equilibrium, it will either monotonically decrease toward the equilibrium, or it will eventually go below equilibrium and then monotonically increase toward the equilibrium. In case (b), if the population is initially above the equilibrium, it will decrease below the equilibrium in one step. If the population is below the equilibrium, it will oscillate above and below the equilibrium getting closer to the equilibrium at every other step, or it will increase monotonically for a while and then start its oscillatory approach to the equilibrium.

3 Sufficient Conditions

While we have the necessary and sufficient condition for global stability of a population model, it is not clear how difficult it might be to verify that this condition is true. Consider, for example, a model in which $f(X)=Xe^{r(1-X)}$. For this model to be globally stable when it is locally stable, we must establish that

$$Xe^{r(1-X)+r(1-Xe^{r(1-X)})}-X>0$$

for all $X\in[1/r,1)$ where $1<r\leqq 2$. It is not immediately evident that this inequality is valid, or how one would establish this inequality. Plotting $f(X)$ when $r=2$, we find that the curve closely resembles the curve in Fig. 1, and we notice that the curve is concave downward up to $x=1$. This suggests a possible condition that $f''(X)<0$ for $X<\bar{X}$, but this condition is not enough since it will not prevent the curve from falling off to 0 too quickly. A limitation on the third derivative of f could prevent this rapid fall off. These considerations suggest the following theorem.

Theorem 2. *If a population model has a maximum X_M in $(0, \bar{X})$ and satisfies*

a) $f''(X)<0$ *for X in* $[X_M, \bar{X})$,

b) $f^{(3)}(X) \geqq 0$ *for all X such that $f''(X)<0$ and $f''(X)$ has at most one sign change,*

c) $|f'(\bar{X})| \leqq 1$ *(the necessary condition for local stability),*

then the model is globally stable.

Proof. From the corollary to Theorem 1, we need to show that (a), (b), and (c) imply that $f(f(X))-X>0$ for all X in $[X_M, \bar{X})$. Let $g(X)=f(f(X))-X$; then $g'(X)=f'(f(X))f'(X)-1$, and $g''(X)=f''(f(X))\,[f'(X)]^2+f'(f(X))f''(X)$. Now $g(\bar{X})=0$, and $g'(\bar{X})=f'(f(\bar{X}))f'(\bar{X})-1=[f'(\bar{X})]^2-1 \leqq 0$. But $g'(X_M)=-1$ since $f'(X_M)=0$. Thus if g' were increasing in the interval (X_M, X), then g' would be negative and g would be decreasing toward 0, so g would be positive and the model would be globally stable. Hence we will establish that $g''(X)>0$ for X in $[X_M, \bar{X})$. From (a) $f''(X)<0$. $f'(X)<0$ and $f'(f(X))<0$ from the assumption of single maximum and the definition of population model. Thus if $f''(f(X))>0$, then $g''(X)>0$. Otherwise $f''(f(X))<0$, and from (b), $f^{(3)}(Y) \geqq 0$ for Y in $[X, f(X)]$. Thus

$$f''(X) \leqq f''(f(X))<0$$

and

$$|f''(X)| \geqq |f''(f(X))|\,. \qquad \text{(P1)}$$

Since f' is decreasing

$$f'(X)>f'(\bar{X})>f'(f(X))\,.$$

But $|f'(\bar{X})| \leqq 1$, so $1>|f'(X)|>|f'(X)|^2$ and

$$|f'(f(X))|>|f'(X)|>|f'(X)|^2\,. \qquad \text{(P2)}$$

Combining inequalities (P1) and (P2)

$$|f''(X)|\,|f'(f(X))|>|f''(f(X))|\,|f'(X)|^2$$

which gives

$$f''(X)f'(f(X))+f''(f(X))\,(f'(X))^2>0\,.$$

Thus $g''(X)>0$ for X in $[X_M, \bar{X})$, and the model is globally stable. □

As we will see when we consider specific models from the literature, the conditions of Theorem 2 are often satisfied and it will be relatively easy to establish that these models are globally stable exactly when they are locally stable. Figure 1 is an example of a model which satisfies the conditions of Theorem 2. Unfortunately, there are some models which do not satisfy these conditions. In particular, the downward concavity condition is not satisfied in some models for all combinations of parameters which are consistent with local stability. One reasonable way to attempt to handle these cases is try to draw a curve that "envelops" the actual curve, and to show that the model corresponding to the enveloping curve is globally stable. One could hope that there would be an enveloping curve which satisfies the conditions of Theorem 2 and that hence it would be easy to establish global stability. Unfortunately, for the models which do not satisfy the conditions of Theorem 2, it is possible to prove that no enveloping curve for these models can satisfy the conditions of Theorem 2.

There are also other reasons to study the ideal of enveloping curves. First, it may be that instead of actually having an analytic expression for a population model, one may have only a set of measured points. If a globally stable enveloping curve can be drawn for the points, then one can be reasonably confident that the measured population obeys a globally stable model. Second, some models may have several parameters. If one can establish that models with larger values of a parameter envelop models with smaller values of that parameter then if the model with a larger value of the parameter is globally stable, one can conclude that models with smaller values of the parameter are also globally stable. In investigating whether local stability implies global stability, one can take the parameter as large as possible consistent with local stability and then try to establish global stability. This should make things easier since you can consider a model with fewer parameters. In some cases, this can result in considering a model with no

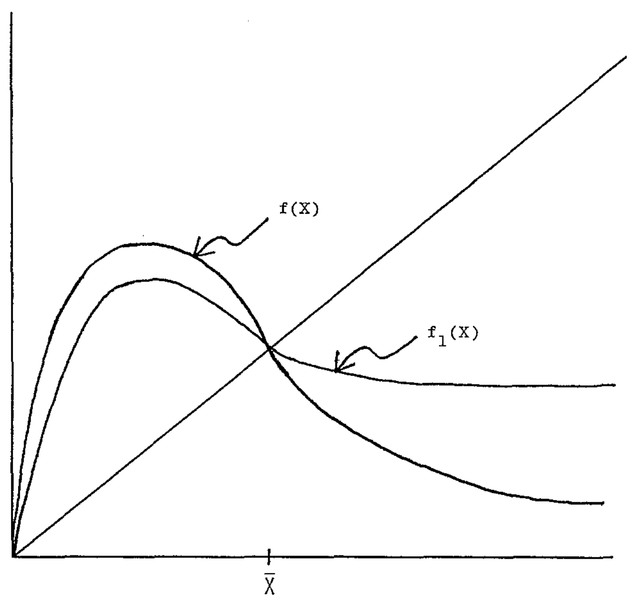

Fig. 4. $f(X)$ envelops $f_1(X)$

parameters, only constants. In more usual cases, this will result in considering a model with one parameter less.

We are now ready for a definition of an enveloping model (see Fig. 4). A population model $X_{t+1}=f(X_t)$ *envelops* a population model $X_{t+1}=f_1(X_t)$ iff

$$f(X)\geqq f_1(X)>X \quad \text{for} \quad \bar{X}>X>0$$

and

$$f(X)\leqq f_1(X)<X \quad \text{for} \quad X>\bar{X}.$$

Theorem 3. *If a globally stable population model envelops a population model, then the enveloped model is also globally stable.*

Proof. If the enveloped model has no maximum less than $\bar{X}$, then this model is globally stable and we do not have to consider the model which envelops it.

If the population model $X_{t+1}=f_1(X_t)$ has a maximum at X_M where $X_M<\bar{X}$, then for any X in $[X_M,\bar{X})$ we have

$$\bar{X}>f_1(f_1(X))\geqq f_1(f(X))\geqq f(f(X))>X.$$

The first inequality follows from the definition of population model. The second inequality follows because f_1 is decreasing and $f(X)\geqq f_1(X)$. The third inequality follows from the second inequality in the definition of envelops. The final inequality follows from the assumption that $f(X)$ corresponds to a globally stable model. □

Corollary. *If there is a parameter P so that*

$$\frac{\partial f}{\partial P}=\begin{cases}+X<\bar{X}\\ -X>\bar{X}\end{cases}$$

and if $X_{t+1}=f(X_t)$ is globally stable when $P=P_0$, then the model is also globally stable for all $P\leqq P_0$ such that the model is a population model.

The corollary follows directly from Theorem 3 because the assumption on P assures that the model with smaller values of P will be enveloped by the model with larger values of P.

When we consider actual models from the literature, we will find that the conditions of Theorem 1 are not satisfied by all models. These conditions are geometric in that they depend on the shape of the curve. While actual models may not satisfy these geometric conditions, the models are still in some reasonable sense "simple". Consider, for example, the model in which $f(X)=Xe^{r(1-X)}$. We could reasonably expect that any model will be similar to this model in that there is a factor of X. Further, we may expect that after we remove this factor, the remaining function will be simple. Since we expect the remaining function to go to 0 for large enough X, we might expect that the reciprocal of this simple function might be even more nicely behaved. This suggests defining $k(X)=X/f(X)$. For our example, we have $k(X)=e^{r(X-1)}$. To capture the idea of simplicity we consider $k'(X)$. For the example, $k'(X)=re^{r(X-1)}$. We find very simple behavior when we consider k/k'. In the example, $k/k'=1/r$. This is the most simple we could hope for, since it is a constant. Other models have more complicated ratios k/k'.

The idea that k/k' will be simple suggests the following not entirely obvious theorem.

Theorem 4. *If a population model with $f'(\bar{X})=-1$ satisfies the following conditions, then the model is globally stable. Using the definition $k=k(X)=X/f(X)$, the conditions are:*

1) $k'\leqq 2$ on $[X_M,\bar{X})$
2) $g(X)\geqq 0$ *where* $k/k'=g(X)+BX$, *and* B *is a constant chosen to make* $g(X)$ *nonnegative*
3) $g'(X)\leqq 0$ on $[X_M,f(X_M)]$
4) $g''(X)\geqq 0$ on $[X_M,f(X_M)]$.

Proof. We will assume that the model is normalized so that $\bar{X}=1$. From the corollary to Theorem 1 we have global stability iff $f(f(X))-X>0$ on $[X_M,1)$. From the definition $k=X/f$, we can rearrange this condition to obtain global stability iff

$$kk(f)<1 \quad \text{on} \quad [X_M,1).$$

Since we have $k(1)=1$, this inequality becomes an equality when $X=1$, and we could establish the inequality if we could show that

$$D[kk(f)]>0 \quad \text{on} \quad [X_M,1).$$

This derivative condition is

$$k'k(f)+kk'(f)f'>0.$$

We may assume that $k'>0$ for all X's of interest because $f'<0$ for these X's. Our condition can be rearranged to

$$\frac{k(f)}{k'(f)}+\frac{k}{k'}f'>0.$$

Since $f'=(k-Xk')/k^2$, we can rearrange this to

$$k\left[\frac{k(f)}{k'(f)}\right]+\frac{k}{k'}-X>0.$$

At $X=1$, the left hand side of this inequality is zero. So we could establish global stability if we could show that the derivative of the left hand side of the above inequality is negative. This derivative condition is

$$k'\left[\frac{k(f)}{k'(f)}\right]+k\left[\frac{k(f)}{k'(f)}\right]'f'+\left[\frac{k}{k'}\right]'-1<0.$$

Expanding kf' as $1-fk'$, this inequality becomes

$$k'\left[\frac{k(f)}{k'(f)}-f\left[\frac{k(f)}{k'(f)}\right]'\right]+\left[\frac{k(f)}{k'(f)}\right]'+\left[\frac{k}{k'}\right]'-1<0.$$

Since the term inside the first set of brackets is positive by conditions (2) and (3), and since $k'\leqq 2$, we can demonstrate this inequality if we can show

$$2\left[\frac{k(f)}{k'(f)}-f\left[\frac{k(f)}{k'(f)}\right]'\right]+\left[\frac{k(f)}{k'(f)}\right]'+\left[\frac{k}{k'}\right]'-1<0.$$

At $X=1$ this is $\frac{2}{k'(1)}-1$, and since $f'(1)=-1$, this is zero. Now all we have to do is to show that the derivative of the left hand side of this inequality is positive. We need

$$(1-2f)f'\left[\frac{k(f)}{k'(f)}\right]''+\left[\frac{k}{k'}\right]''>0.$$

But this is valid because $f>1$ and $f'<0$ on $(X_M, 1)$ and by condition (4) $[k/k']''\geqq 0$ on $[X_M, f(X_M)]$. □

4 Models

In this section, we will consider a number of models which have appeared in the literature. We will use our theorems to show that all of these models are globally stable if they are population models according to our definition and they satisfy the necessary condition for local stability. Specifically, for the following models we find global stability when $-1\leqq f'(\bar{X})<1$. When $f'(\bar{X})=1$, these models degenerate to $X_{t+1}=X_t$, which is not globally stable, and which is not a population model according to our definition. It is pleasant to find that our methods establish global stability even when $f'(\bar{X})=-1$, a case in which the usual linear method for even local stability is insufficient.

Model I:

$f(X)=X\exp[r(1-X)]$

$f'(X)=(1-rX)\exp[r(1-X)]$

$f''(X)=-r(2-rX)\exp[r(1-X)]$

$f^{(3)}(X)=r^2(3-rX)\exp[r(1-X)]$

$\partial f/\partial r=X(1-X)\exp[r(1-X)]$

$k(X)=\exp[r(X-1)]$

$k/k'=1/r=g(X)+BX$

$g(X)=1/r, \quad B=0.$

Parametric region of stability: $0<r\leqq 2$.

Global stability for this model can be established in several ways. Local stability implies that $0\leqq r\leqq 2$. For $r=0$, the model degenerates to $f(X)=X$, which is not a population model and is not globally stable. For $0<r\leqq 1$, the maximum does not occur before the equilibrium point, so by the corollary to Theorem 1 the model is globally stable. For $1<r\leqq 2$, f'' is negative on $[X_M, 1)$ and $f^{(3)}$ is positive when f'' is negative, so by Theorem 2 the model is globally stable. The parameter r satisfies the conditions of the corollary to Theorem 3, so the model is globally stable for $0<r\leqq 2$ because the model is globally stable for $r=2$. Global stability for $r=2$ can be established by Theorem 2 as we have done above, or by Theorem 4 since it is easy to check that the derivatives of g are 0.

This model has been widely discussed in the literature, for example by Moran (1950), Ricker (1954), Smith (1974), May (1974), and Fisher et al. (1979).

Model II:

$f(X)=X[1+r(1-X)]$

$f'(X)=1+r-2rX$

$f''(X)=-2r$

$f^{(3)}(X)=0$

$\partial f/\partial r=X(1-X)$

$k(X)=1/[1+r(1-X)]$

$k/k'=\frac{1+r}{r}-X=g(X)+BX$

$g(X)=(1+r)/r, \quad B=-1.$

Parametric region of stability: $0<r\leqq 2$.

As for the previous model, the global stability of this model can be established in several ways. Local stability implies that $0\leqq r\leqq 2$. For $r=0$, the model is degenerate. For $0<r\leqq 1$, this model is globally stable by the corollary to Theorem 1. For $1<r\leqq 2$, $f''<0$ and $f^{(3)}=0$, so global stability follows from Theorem 2. The parameter r satisfies the conditions of the corollary to Theorem 3, so global stability for $0<r\leqq 2$ follows from the global stability for $r=2$, which follows from Theorem 2 above or from the conditions of Theorem 4.

Unlike the previous model, in this model $f(X)$ goes to 0 for finite X, so we should more correctly write $f(X)=\max\{x[1+r(1-X)], 0\}$. We should also recall that global stability here means that for all X such that $f(X)>0$, $f^k(X)$ converges to the equilibrium point.

This model has also been widely discussed in the literature, for example by Smith (1968).

Model III:

$f(X)=X[1-r\ln X]$

$f'(X)=1-r-r\ln X$

$f''(X)=-r/X$

$f^{(3)}(X)=r/X^2$

$\partial f/\partial r=-X\ln X$

$k(X)=1/[1-r\ln X]$

$k/k'=X(1-r\ln X)/r=g(X)+BX$

$g(X)=-X\ln X, \quad B=1/r.$

Parametric region of stability: $0<r\leqq 2$.

As in the previous two models, local stability implies that $0\leqq r\leqq 2$, but when $r=0$ the model degenerates. This model is globally stable for $0<r\leqq 2$ because when $0<r\leqq 1$ no maximum occurs in (0, 1), and when $1<r\leqq 2$ the conditions of Theorem 2 are satisfied. The method of Theorem 4 cannot be used to prove this model globally stable because $g''(X)<0$. As in Model II, this model should really be written as $f(X)=\max\{X[1-r\ln X], 0\}$, because $1-r\ln X$ becomes negative for large enough X.

This model is studied in Nobile et al. They claim and demonstrate that this model is globally stable for $0<r\leqq 1$. They claim but do not demonstrate that this model is globally stable for $1<r<2$. They omit mention of the case when $r=2$. We have used the version of their model which is normalized so that $\bar{X}=1$, while they mainly discuss the version in which $f(X)=-rX\ln X$. The same conclusions about global stability hold for both versions of the model.

Model IV:

$f(X)=X[1/(b+cX)-d]$

$f'(X)=b/(b+cX)^2-d$

$f''(X)=-2bc/(b+cX)^3$

$f^{(3)}(X)=6bc^2/(b+cX)^4$

$\bar{f}(X)=X[(d+1)/[b(d+1)+(1-b(d+1))X]-d]$

$$\partial\bar{f}/\partial b=-(d+1)^2X(1-X)/[b(d+1)+(1-b(d+1))X]^2$$

$$\bar{k}(X)=[b(d+1)-[1-b(d+1)]X]/[(d+1)\times(1-bd)-d[1-b(d+1)]X]$$

$$\bar{k}/\bar{k}'=\{[b(d+1)+[1-b(d+1)]X]\times[(d+1)(1-bd)-d[1-b(d+1)]X]\}/(d+1)[1-b(d+1)].$$

Parametric region of stability:

$(d-1)/(d+1)^2\leqq b<1/(d+1).$

For this model, local stability implies

$(d-1)/(d+1)^2\leqq b\leqq 1/(d+1),$

but for $b=1/(d+1)$ the model degenerates because it has no positive equilibrium point. The parameter c does not appear because it determines the location of the equilibrium point but does not affect the stability. It is easy to check that this model has no maximum in $(0,\bar{X})$ or that the model satisfies the conditions of Theorem 2, and thus in either case the population model is globally stable. We have also given $\bar{f}$ which is normalized so that $\bar{X}=1$. Notice that c does not appear in $\bar{f}$. The dependence of $\bar{f}$ on b is exactly the reverse of what is needed for the corollary to Theorem 3, so the models with smaller values of b envelop the models with larger values of b. Theorem 4 cannot be used to demonstrate global stability for this model since the second derivative of $\bar{k}/\bar{k}'$ is negative.

As for the previous two models, $f(X)$ becomes negative for large enough X, and we recall that global stability is only for those X's such that $f(X)>0$.

This model is from Utida (1957).

Model V:

$f(X)=\lambda X/(1+a\exp(bX)), \quad \lambda=1+a\exp(b)$

$f'(X)=\lambda[1+(1-bX)a\exp(bX)]/(1+a\exp(bX))^2$

$$f''(X)=-\lambda ab\exp(bX)[(1-a\exp(bX))bX+2(1+a\exp(bX))]/(1+a\exp(bX))^3$$

$$f^{(3)}(X)=-\lambda ab^2\exp(bX)\{(1+a\exp(bX))\times[1+(1-bX)a\exp(bX)]-3a\exp(bX)[Xb(1-\exp(bX))+2(1+a\exp(bX))]\}/(1+a\exp(bX))^4$$

$\partial f/\partial a=X\exp(b)[1-\exp(b(X-1))]/[1+a\exp(bX)]^2$

$k(X)=[1+a\exp(bX)]/[1+a\exp(b)]$

$k/k'=\exp(-bX)/ab+1/b$

$g(X)=k/k', \quad B=0$

$g'(X)=-\exp(-bX)/a$

$g''(X)=b\exp(-bX)/a$

Parametric region of stability:

$a(b-2)\exp(b)\leqq 2, \quad a>0, \quad b>0.$

Local stability gives the above parametric region of stability but would allow $a=0$ or $b=0$, which are ruled out because the model would degenerate to $f(X)=X$.

The term in square brackets in $f'(X)$ is decreasing so there is at most one maximum in (0, 1). If there is no maximum, the model is globally stable. If there is a maximum, we can follow Theorem 2 to argue that the model is globally stable. If there is a maximum, then the term inside the square brackets in $f''(X)$ will be decreasing, so if f'' becomes positive it will remain positive. $f''(1)$ will be negative iff $(1-a\exp(b))b+2(1+a\exp(b))>0$, but the sufficient condition for local stability assures that this will occur. If $X>X_M$, then the first term in square brackets in $f^{(3)}(X)$ is negative. If X is before the change in concavity, the second term in square brackets is positive as we have argued above. So $f^{(3)}(X)>0$ up to the change of concavity and hence by Theorem 2 the model is globally stable.

The model for larger values of the parameter a envelops the models for smaller values of a. This fact and the above computations of $g(X)$ and its derivatives show that this model obeys the conditions of Theorem 4 and hence the model is globally stable.

Although either Theorem 2 or Theorem 4 can be used to show that this model is globally stable, it seems much easier in this case to use Theorem 4. This is unlike previously considered models in which Theorem 2 was easier to apply than Theorem 4.

This model is from Pennycuick et al. (1968).

Model VI:

$$f(X)=\lambda X/(1+aX)^b, \quad \lambda=(1+a)^b$$
$$f'(X)=\lambda[1-a(b-1)X]/(1+aX)^{b+1}$$
$$f''(X)=-\lambda ab[2-a(b-1)X]/(1+aX)^{b+2}$$
$$f^{(3)}(X)=\lambda a^2b(b+1)[3-a(b-1)X]/(1+aX)^{b+3}$$
$$\partial f/\partial a=X(1-X)b(1+a)^{b-1}/(1+aX)^{b+1}$$
$$k(X)=(1+aX)^b/\lambda$$
$$k/k'=(1+aX)/ab=g(X)+bX$$
$$g(X)=\frac{1}{ab}, \quad B=1/b.$$

Parametric region of stability:

$$ab\leqq 2(1+a), \quad a>0, \quad b>0.$$

The parametric region of stability agrees with the region implied by local stability except that $a=0$ or $b=0$ is not included because in these cases the model degenerates into $f(X)=X$.

Theorem 2 cannot be used to demonstrate the global stability of this model because there are parameter values which give local stability but allow $f''(X)$ to become positive before the equilibrium point.

Theorem 4 was created to deal with this model. It is evident from $\partial f/\partial a$ that this model with larger values of a envelops the models with smaller values of a. The other conditions of Theorem 4 are evidently met, so this model is globally stable.

The parameter b could be used instead of the parameter a as an enveloping parameter. However, if one takes a at its largest value consistent with local stability, the remaining parameter b no longer serves as an enveloping parameter. In fact, with $a=2/(b-2)$, $\partial f/\partial b>0$ for all values of X. One could show that $f(f(X))-X$ is a decreasing function of b for $X\in[X_M, 1)$, but this computation is rather involved.

This model is from Hassell (1974).

Model VII:

$$f(X)=\lambda X/(1+(\lambda-1)X^c)$$
$$f'(X)=\lambda[1-(c-1)(\lambda-1)X^c]/[1+(\lambda-1)X^c]^2$$
$$f''(X)=-\lambda(\lambda-1)cX^{c-1}[c+1-(c-1)\times(\lambda-1)X^c]/[1+(\lambda-1)X^c]^3$$
$$\partial f/\partial\lambda=X(1-X^c)/[1+(\lambda-1)X^c]^2$$
$$k(X)=[1+(\lambda-1)X^c]/\lambda$$
$$k/k'=1/c(\lambda-1)X^{c-1}+X/c$$
$$g(X)=1/c(\lambda-1)X^{c-1}, \quad B=1/c$$
$$g'(X)=-(c-1)/c(\lambda-1)X^c$$
$$g''(X)=(c-1)/(\lambda-1)X^{c+1}.$$

Parametric region of stability

$$c(\lambda-1)\leqq 2\lambda, \quad \lambda>1, \quad c>0.$$

The parametric region of stability follows from the necessary conditon for local stability, except that $\lambda=1$ or $c=0$ result in the degenerate model $f(X)=X$. As in the last model, Theorem 2 cannot be used to demonstrate global stability because there are parameter values which are consistent with local stability but allow f'' to become positive before the equilibrium point. On the other hand, it is easy to check that the conditions of Theorem 4 are satisfied, so the model is globally stable. Yet another way to prove the global stability of this model is to use the transformation $X^c\to Z$, $\lambda-1\to a$ on the c^{th} power of the model, i.e.,

$$X_{t+1}^c=(1+a)^cX^c/(1+aX^c)^c$$

giving

$$Z_{t+1}=(1+a)^cZ/(1+aZ)^c.$$

Since this transforms this model into Model VI, the global stability of this model follows from the global stability of Model VI.

This model is from Smith (1974).

5 Discussion

Population modelers are well aware of the sufficient condition for local stability. After considering local stability, however, they often imply that global stability follows. As we have demonstrated, this is not always the case.

While the condition for local stability is simple, demonstrating global stability may be quite difficult. To prove global stability one usually constructs a specific function, called a Liapunov function, for a specific model and demonstrates that the Liapunov function satisfies a number of conditions related to the model. The general case of Liapunov functions and difference equations is discussed in LaSalle (1976). Construction of Liapunov functions for specific population models appears in Fisher et al. (1979) and Goh (1979).

We have demonstrated that population models are special enough to have a simpler necessary and sufficient condition for global stability. This condition is: the model has no cycle of period 2, or even more specifically, $f(f(X))>X$ on $[X_M, \bar{X})$. Difference equations more general than our population models may have no cycle of period 2 and yet fail to be globally stable.

Unfortunately, the lack of cycles of period 2 may not be very easily testable, so we gave the sufficient (but not necessary) methods of Theorems 2 and 4, which are easier to test. These methods are useful for the actual models we culled from the literature, but it is certainly possible that there are other population models for which these methods are not useful.

We have also demonstrated that there are models which satisfy the definition of population model and are locally but not globally stable. We have a seeming paradox: on the one hand, population models do not need to have local and global stability coincide, but on the other hand, *all* the actual population models from the literature do have local and global stability coinciding. Clearly there is something extra about models from the literature which has not been captured in our definition of population model. As far as we can see, this something extra is that the actual models are simple in that they involve only elementary functions like polynomials, exponentials and logs, and use at most one division. Whether this idea of "simplicity" can be explicitly tied down we leave as an open question. Tying down this idea of simplicity may not be easy because the actual models seem to be of rather different types. One could say that two models $f_1(X)$ and $f_2(X)$ are of the same type if there is a function φ so that $f_1(X)=\varphi(f_2(\varphi^{-1}(X))$. While Models VI and VII are of the same type, they are not of the same type as Model I. The methods used to prove global stability could also be used to attempt to classify models. Both Theorem 2 and Theorem 4 can be used on Models I, II, and V. Theorem 2 but not Theorem 4 can be used on Models III and IV. Theorem 4 but not Theorem 2 can be used on Models VI and VII. This suggests that there may be a number of different kinds of population models, and no single simple method may be sufficient to analyze all of the different models.

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Received: July 4, 1985

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