

Model Stability and Instability in Age Structured Populations

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Primary sources of instability and oscillation in the dynamics of a single species are various mechanisms which cause delayed responses of fecundity to environmental changes. Fundamental mechanisms include gestation periods, age-specific reproductive rates and age-specific (or weighted) effects of population density on fecundity. The effects on the stability and instability of equilibria caused by these three specific mechanisms are studied by means of a general model equation.

1. Introduction

It is by now a firmly established tenet in population dynamics that “time delays” in a species’ response to any change in its environment can destabilize its dynamical equilibrium. This principle has been widely expressed in the literature and has found support both in experimental studies (e.g. see Slobodkin, 1961; Nicholson, 1954; Fujii, 1968; Pratt, 1943; Beddington, 1974) and in theoretical work (May, 1974, 1976; May, Conway, Hassell & Southwood, 1974; Cushing, 1977, 1978). “Time delay” is a very broad and unspecific term and it should be clear to even a casual observer that there can be a great variety of quite different and unrelated mechanisms which can cause delayed responses in population dynamics. Perhaps the most obvious mechanisms are those related to the time necessary for the production of a new reproducing generation, primarily gestation and maturation periods. This “generation time”, which is often referred to in discussions concerning delays (May, 1976; May *et al.*, 1974), is essentially inherent to the population, although it can be affected by such environmental factors as temperature, resource availability and quality, etc. Beyond these primary delay mechanisms, which concern the fecundity or per unit birth rate of the population as opposed to the mortality or per unit death rate, there are many others which can cause delayed responses in the population’s density dependent vital parameters. Some of those which have been mentioned in

the literature include age-specific resource consumption rates which cause a delay in the effect that a newborn has on the supply of resources available to other members of the population (Slobodkin, 1961); the accumulating polluting effects of all past members of the population (Volterra, 1934; Kostitzin, 1939); the generation time of a resource or prey species (May, 1974); and delays in behavioral responses to changes in resource or prey availability, for example hunger thresholds or satiation limits or such learned behavior as predator search or prey-switching patterns (Ricklefs, 1973). Even this short list of delay causing mechanisms is enough to demonstrate the complexity and difficulty inherent in the attempt to study the role of delays in population dynamics in any detail and depth beyond the familiar crude and oversimplified principle that "delays destabilize".

The purpose of this paper is to investigate mathematically the stability and instability of population equilibria as they depend specifically on gestation and maturation periods and on age specific density effects on fecundity. I have chosen to concentrate on these specific delay mechanisms because they seem to be primary ones and because they have been mentioned by biologists as destabilizing agents in certain experiments (e.g. see Slobodkin, 1961, ch. 9). For this same reason as well as the reason that, to quote Ricklefs (1973, p. 488): "time lags might be expected to occur primarily in stabilizing processes involving reproduction rather than death, because death is an immediate response to environmental change", I will not be concerned with any delays in death rate responses. This is not to say, of course, that under certain circumstances for some populations delays in the death rate response or other delays cannot be more important or significant.

The analysis will be done using a non-linear model of age-dependent population growth which is based on a partial differential equation (sometimes referred to as von Foerster's equation) and in which the fecundity function is assumed to be a functional of the age specific population density. The model is a modification of the very general models considered by Hoppenstaedt (1975) and Rotenberg (1975), a modification which includes a gestation period probability density function. The model is also a generalization of a model of Swick (1977) in which a fixed constant gestation period is assumed. It will be assumed here that all vital parameters are time independent and that age-specific fecundity is a decreasing functional of population density. Since the analysis will be confined to a linearized stability analysis, the fecundity function will in fact be assumed to be a specific linear decreasing functional of density (higher order non-linearities having qualitatively little effect locally near equilibrium) exactly as is done by Hoppenstaedt (1975, p. 9).

By consideration of a variety of cases based upon this model the following main conclusions will be drawn. A gestation period can readily be a cause of instabilities in the sense that such a delay can easily, in even very simple models, cause an otherwise stable equilibrium to become unstable provided it is sufficiently long relative to other relevant time scales (see section 4.C). With regard to maturation periods, however, the situation is much more subtle and complex. Age differentials in reproductive output do not necessarily lead to instabilities even if the "maturation delay" is long. It will be shown in section 4.A, for example, that if fecundity is a function of the present total population size alone or of the present total birth rate alone (i.e. of the class of newborns alone) then the equilibrium is in fact always stable regardless of any age-specific differentials in reproductive output. On the other hand, if the response of fecundity is sufficiently weighted towards an older age group then instabilities can occur as is shown in section 4.B. This may occur for example if an individual's fecundity is primarily affected by the presence of other individuals of the same age. This could occur in species for which an individual's competition for resources is primarily with members of his own age cohort, say for example in an insect species whose generations are synchronized to appear separately and whose larval and adult members feed on different resources. A particularly interesting case occurs when fecundity of an individual depends heavily on the birth rate of the total population at the time of the birth of the individual. Not only can instabilities result in this case, as is seen in section 4.D, but the limiting case when density dependence is concentrated solely on the birth rate at the time of birth results in difference equation models whose solutions exhibit chaotic behavior. Specifically, the well known discrete time logistic equation can under these circumstances be derived from the model equation (14) considered in section 4.D below.

Thus the stability vs. instability question, in so far as it concerns age-specific fecundity, is intimately tied up with not only the differences in reproductive capabilities of different age classes but also with the nonlinear nature of the effect on fecundity of changes in population density and neither of these phenomena alone can in general be said necessarily to contribute instabilities to a model equilibrium. In fact, in at least one case investigated below (see section 4.E), the presence of a large maturation or gestation period can under certain circumstances stabilize what would otherwise be an unstable equilibrium.

We see then that a delay caused by the often referred to "generation time" is upon close investigation a complicated phenomenon caused in even simple cases by several independent mechanisms and that it is difficult if not impossible to make broad generalizations about its instability causing

properties. It is certainly inadequate simply to place a time lag in one's favorite differential equation model in order to study such a phenomenon in any general way. For a fuller discussion of this point and the relationship between "generation time" delays and time delay differential equations, at least when fecundity depends on total population size, see Cushing (1979*b*). A case in point is the overworked delay logistic equation, originally due to Volterra (1934), which can easily be seen to be totally inappropriate as a model involving gestation or maturation delays. Volterra was originally interested in an entirely different delay mechanism, a delay in the death rate caused by accumulating pollutants from past population members.

As an equilibrium of a non-linear autonomous model passes from a stable to an unstable state as some parameter varies through a critical value one expects to see undamped, sustained oscillations occurring. This will be the case in the models considered here. This interesting bifurcation phenomenon is rigorously studied for integral equations considered in this paper by Cushing (1979*a*) and Cushing & Simmes (1979). Attention will be restricted in this paper, however, only to the question of stability versus instability.

2. The Model and Its Reduction to an Integral Equation

Suppose that the female population of a single isolated species can be described by an age-dependent density function $n = n(t, a)$ of time t and age $a \geq 0$. Thus the density of individuals between ages a_1 and a_2 at time t is $\int_{a_1}^{a_2} n(t, a) da$. If t and a are measured on the same scale and if n is differentiable, then $\partial n / \partial t + \partial n / \partial a$ is the change in the age class a at time t . Suppose that this change is proportional to the present density so that if $d = d(a) \geq 0$ is the age specific, per unit *death rate* then

$$\partial n / \partial t + \partial n / \partial a = -d(a)n, a \geq 0. \quad (1)$$

Equation (1) [essentially due to McKendrick (1926)] accounts for all removals from the population under the assumption that there is no way to leave the population except by death. In order to account for additions to the population, which is assumed possible only by birth, an age specific *fecundity function* $f = f(t, a)$ is defined which yields the per unit number of eggs produced by females of age a . In this paper the dependence of f on time t is assumed to be only implicit through a functional dependence on the density function n . More specifically, throughout this paper it will be assumed that

$$f(t, a) = b\beta(a) \left[1 - \int_0^{\infty} w(a, \sigma) n(t, \sigma) d\sigma \right]_+, \quad (2)$$

where $b > 0$ is a constant, $\beta(a) \geq 0$ is a normalized age specific fecundity function for the population in the absence of density effects (i.e. for low densities) and $w(a, \sigma) \geq 0$ is a weighting function which describes the weighted effect that each age class has on the fecundity of females of age a . The function $\beta(a)$ will be called the *maturation function* and the constant b will be called the *(inherent) birth modulus*. The notation $[\cdot]_+$ means $[x]_+ = x$ if $x \geq 0$ and $[x]_+ = 0$ if $x < 0$.

Thus the birth process for the population can be written

$$n(t, 0) = \int_{s=-\infty}^t g(t-s) \int_{a=0}^{\infty} f(s, a)n(s, a) da ds, \tag{3}$$

where $g(s) \geq 0, \int_0^{\infty} g(s) ds = 1$ is a *gestation period probability density function* which describes the probability that an egg laid at any time will produce a (female) member of the population s units of time later.

It will be assumed that the population has been evolving for a considerable (in fact infinite) amount of time. Equations (1)–(3) are then to be solved for $-\infty < t < +\infty$. Alternatively one could pose an initial value problem by prescribing an initial age distribution $n(0, a)$ at time $t = 0$ and then solve (1)–(3) for $t > 0$. This would introduce transients into the equation and (presumably) the solutions and would considerably complicate the resulting technical manipulations and equations. In order to simplify the mathematical considerations initial conditions will be ignored or “placed at $t = -\infty$ ” and only the resulting “limiting or asymptotic” model considered.

The first-order partial differential equation (1) can be easily integrated to obtain

$$n(t, a) = B(t-a) \exp[-D(a)], \quad a > 0, -\infty < t < +\infty, \tag{4}$$

where $D(a) := \int_0^a d(s) ds$ and $B(t) := n(t, 0)$. Equation (4) does not provide a solution of (1)–(3) because the unknown density n appears on the right hand side through the *birth rate* function $B(t)$. The birth equation (3), together with (4), yields an integral equation

$$B(t) = \int_{s=-\infty}^t g(t-s) \int_{a=0}^{\infty} b\beta(a) \times \left[1 - \int_{\sigma=0}^{\infty} w(a, \sigma) B(s-\sigma) e^{-D(\sigma)} d\sigma \right]_+ B(s-a) e^{-D(a)} da ds \tag{5}$$

to solve for $B(t)$. Any solution $B(t)$ of (5) gives a solution of the model equations (1)–(3) by means of (4).

3. Equilibria

We are interested in equilibrium states, i.e. time independent solutions of the model equations (1)–(3). These are given by constant birth rates $B(t) \equiv B_\infty > 0$ as solutions of the equation (5):

$$B_\infty = b \int_{a=0}^{\infty} \beta(a) \left[1 - B_\infty \int_{\sigma=0}^{\infty} w(a, \sigma) e^{-D(\sigma)} d\sigma \right]_+ B_\infty e^{-D(a)} da.$$

Thus either $B_\infty = 0$ or $B_\infty = (R - 1)/S$ where

$$R := b \int_0^{\infty} \beta(a) e^{-D(a)} da$$

and

$$S := b \int_0^{\infty} \beta(a) \int_{\sigma=0}^{\infty} w(a, \sigma) e^{-D(\sigma)} d\sigma e^{-D(a)} da > 0.$$

The constant R is the *net reproductive rate* and equals the expected number of (female) offspring during the lifespan of a (female) member of the population when density effects are absent or in other words when population densities are low. The quantity S is a modified net reproductive rate in which the fecundity function $b\beta(a)$ in R has been replaced by a modified fecundity $b\beta(a) \int_{\sigma=0}^{\infty} w(a, \sigma) e^{-D(\sigma)} d\sigma$ which depends upon the density weighting function w .

In order for there to exist a positive equilibrium it is seen to be necessary and sufficient that $R > 1$.

In order to study the local stability properties of B_∞ by means of the principle of linearized stability, let $B(t) = x(t) + B_\infty$, substitute into (5) and ignore all “higher order”, that is all but linear terms in x in the resulting equation. This yields the integral equation

$$x(t) = \int_{s=-\infty}^t k(t-s)x(s) ds, \quad (6)$$

where

$$\begin{aligned} k(t) &:= \int_{\sigma=0}^t g(t-\sigma)h(\sigma) d\sigma \\ h(\sigma) &:= b \left\{ \beta(\sigma) \left[1 - B_\infty \int_{s=0}^{\infty} w(\sigma, s) e^{-D(s)} ds \right] \right. \\ &\quad \left. - B_\infty \int_{a=0}^{\infty} \beta(a) w(a, \sigma) e^{-D(a)} da \right\} e^{-D(\sigma)}. \end{aligned}$$

It is a bit difficult to ascribe a precise biological meaning to the two

expressions $k(t)$ and $h(\sigma)$ as they are given by these formulas in terms of the quantities g, β, b, d and w . However, observing that equation (6) is a “renewal” type integral equation we see that the kernel $k(t)$ can be interpreted, in this linearized model at least, as follows. The function $h(\sigma)$ can be considered to be the per unit density egg-laying fecundity per unit time at age $\sigma, 0 \leq \sigma \leq t$, multiplied by the probability of surviving to age σ . Thus, $h(\sigma)x(s) ds$ yields the total egg production rate (in excess of the equilibrium) per unit time due to individuals of age σ who were born at time s and $g(t-\sigma)h(\sigma) d\sigma$ then gives the fraction of these eggs hatching at time t . The integral in (6) is thus the total birth rate at time t due to egg contributions from all individuals born at all possible past times s .

Associated with equation (6) is the *characteristic function*

$$\Delta(z) := 1 - k^*(z) \quad \text{where} \quad k^*(z) := \int_0^\infty e^{-zt} k(t) dt.$$

Note that by the convolution theorem for Laplace transforms $k^*(z) = g^*(z)h^*(z)$. If and in fact only if the Paley-Wiener condition,

$$\Delta(z) := 1 - k^*(z) \neq 0 \quad \text{for} \quad \text{Re } z \geq 0, \tag{7}$$

is satisfied, is equation (6) and hence the equilibrium B_∞ of (5) stable. By stability is meant that if $x(t)$ is small for all $t \leq t_0$ then $x(t) = B(t) - B_\infty$ is small for $t \geq t_0$ and $x(t) \rightarrow 0$ as $t \rightarrow +\infty$. If (7) fails to hold then equation (6) is unstable. For all this to be true it is necessary to assume $\int_0^\infty |k(t)| dt < +\infty$.

In the following section the stability condition (7) will be investigated for a variety of special cases.

4. Stability and Instability

The goal as explained in the Introduction is to study the stability and instability of population equilibria as they depend on the gestation function $g(s)$, the maturation period as described by $b\beta(a)$ and the age specific density effects on fecundity as described by the weighting function $w(a, \sigma)$. One can see by the complicated manner in which these entities enter into the characteristic function $\Delta(z)$ it is very unlikely that any broad, general conclusions concerning the stability or instability of equilibria can be made in the general model (1)–(3). For this reason as well as in order to focus attention on various individual phenomena in isolation from others I will now turn to some special cases. In all of these cases the simplifying assumption that $d(a) \equiv d = \text{constant} > 0$ will be made. Note then that $R = b\beta^*(d)$. The special cases to be considered can be broken into five categories which are summarized in Table 1 appearing in the section 5.

(A) STABLE CASES WITH MATURATION, BUT NO GESTATION PERIODS

Let $g(s) = \delta_0(s)$, the Dirac delta function at $s = 0$, in order to consider the case of no gestation period. Such a model could be appropriate for populations with short gestation periods. Let $w(a, \sigma) = w(\sigma) \geq 0$ be independent of age a . This means that whereas different age classes may very well have different negative effects on fecundity because of age specific differentials in resource consumption, the total weighted effect of all age classes on the fecundity of any age class is the same for all age classes.

Under these circumstances, assuming $R := b\beta^*(d) > 1$ so that the equilibrium

$$B_\infty = \frac{b\beta^*(d) - 1}{b\beta^*(d)w^*(d)} \quad (8)$$

is positive, the stability condition (7) reduces to

$$1 + (R - 1) \frac{w^*(z + d)}{w^*(d)} \neq \frac{\beta^*(z + d)}{\beta^*(d)} \quad \text{for } \operatorname{Re} z \geq 0. \quad (9)$$

At this point it is still possible, as we will see below in 4B, that (9) fail to hold. Under some further special assumptions, however (9) will always hold.

For example, suppose $w(a, \sigma) \equiv w_0 = \text{constant} > 0$ so that fecundity is a function of the present *total population size* $\int_0^\infty n(t, a) da$ and hence all age classes contribute equally to the density restraints on fecundity. [See Cushing (1979b) for more details of this important special case.] Then $w^*(z) = w_0/z$ and the stability condition (9) becomes

$$\frac{z + dR}{z + d} \neq \frac{\beta^*(z + d)}{\beta^*(d)} \quad \text{for } \operatorname{Re} z \geq 0. \quad (10)$$

Inasmuch as $|z + dR|/|z + d| > 1$ when $R > 1$ while $|\beta^*(z + d)| \leq |\beta^*(d)|$ for $\operatorname{Re} z \geq 0$ it follows that the stability condition (10) holds.

Thus, *in the absence of a gestation period and in the case when fecundity depends on the present total population size, the unique positive equilibrium (8) of equation (5) is stable for any maturation function $\beta(a)$ and birth modulus $b > 0$ in the fecundity function (2) and for any age independent death rate $d > 0$.*

The same conclusion can be drawn if fecundity is a function, not of the present total population size, but of the present birth rate $B(t)$. To see this let $w(a, \sigma) = w_0\delta_0(\sigma)$, $w_0 = \text{constant} > 0$, in which case

$$f(t, a) = b\beta(a)[1 - w_0B(t)]_+.$$

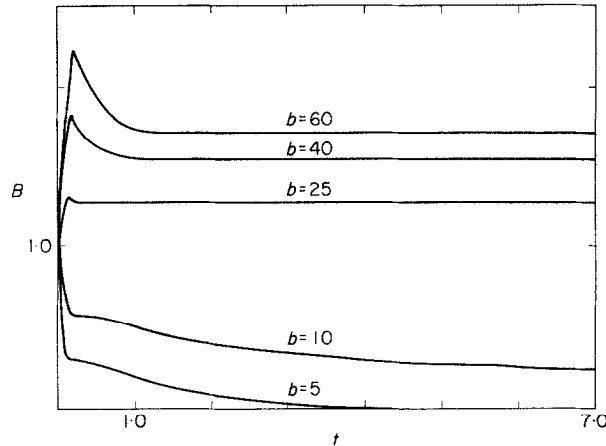


FIG. 1. Five numerically computed solutions $B(t)$ of equation (5) are shown plotted against time $t \geq 0$ when $g(s) = \delta_0(s)$, $w(a, \sigma) = 1$, $d(a) = 2$ and $\beta(a) = a e^{-a}$. The equilibrium $B_\infty = 2(b - 9)/b$ is positive if and only if $b > 9$. In the case when the birth modulus $b = 5$ there is no positive equilibrium and the computed solution tends to zero as $t \rightarrow +\infty$. All other cases shown illustrate the stability of the positive equilibria. These solutions illustrate the stability of positive equilibria when fecundity depends on total population size and there is no gestation period in model equation (5).

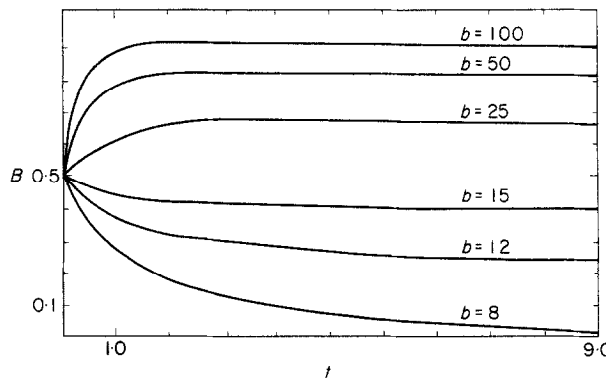


FIG. 2. Six numerically integrated solutions $B(t)$ of equation (5) are shown for $g(s) = \delta_0(s)$, $w(a, \sigma) = \delta_0(\sigma)$, $d(a) = 2$ and $\beta(a) = a e^{-a}$. The equilibrium $(b-9)/b$ is positive if and only if $b > 9$. The case when $b = 8$ shows the solution tending to zero as $t \rightarrow +\infty$. All other cases demonstrate the stability of the equilibrium when $b > 9$. These solutions illustrate the stability of positive equilibria when fecundity depends on the present total birth rate and there is no gestation period in model equation (5).

Since $w^*(z) = w_0$ in this case the stability condition (9) is simply

$$R \neq \frac{\beta^*(z+d)}{\beta^*(d)} \quad \text{for } \operatorname{Re} z \geq 0$$

and again is seen to be valid (since $R > 1$ and the right hand side, just as in the previous case, is in magnitude not greater than 1 for $\operatorname{Re} z \geq 0$).

Thus, *the above conclusion remains true if the assumption that fecundity depends on present total population is replaced by the assumption that fecundity depends on the present birth rate.*

These two conclusions are illustrated by numerically integrated examples in Figs 1 and 2.

(B) AN UNSTABLE CASE WITH A MATURATION, BUT NO GESTATION PERIOD

The above two stable cases in 4.A may be viewed in a certain sense as two opposite extremes: in the first case fecundity depends in a non-age specific way only on total population size while in the second case only newborns affect fecundities, presumably because they consume resources in far greater proportion to their numbers than does any other age class. Age-specific differential resource consumption has been explicitly mentioned as a source of instability as observed in laboratory experiments with insect populations (Slobodkin, 1961) and consequently we might expect to see instability for (5) in certain circumstances under even the simplifying assumptions made in 4.A above. That such an instability can indeed occur in (5) will be shown by means of a specific example.

The distribution functions

$$p_{n,T}(a) := \frac{1}{n!} \left(\frac{n}{T}\right)^{n+1} a^n \exp(-na/T), \quad n = 1, 2, 3, \dots \quad (11)$$

are frequently used in models in which a non-negative function with a unique maximum is desired with monotonic decay to zero as $a \rightarrow +\infty$ (see for example Cushing, 1977; Rotenberg, 1975; MacDonald, 1978). The maximum of $p_{n,T}(a)$ occurs at $a = T$ and the integer n reciprocally measures the "width" of the peak. These distributions are normalized so that $\int_0^\infty p_{n,T}(a) da = 1$. Also $p_{n,T}^*(z) = [n/(Tz+n)]^{n+1}$.

Suppose that in the model described in 4.A above one takes the simplest case $n = 1$: $\beta(a) = p_{1,1}(a)$ and $w(a, \sigma) = p_{1,T}(\sigma)$. This means first of all that maximum reproductive output occurs at age $a = 1$ and that reproductive output, while dropping to zero at $a = 0$ and $+\infty$, is nonetheless rather broadly spread throughout age classes. Secondly, with regard to density

effects on fecundity the age class $\sigma = T$ has the greatest weighted effect, but again these effects are rather broadly distributed throughout the age classes.

In this case $R = b/(d + 1)^2$ so that the equilibrium (8) is positive if and only if $b > (d + 1)^2$. The stability condition (9), after some algebraic manipulation, is seen to be equivalent to

$$T^2 z^4 + 2T(2dT + T + 1)z^3 + (dT + 1)(4dT + RdT + 4T + R)z^2 + 2R(d + 1)(dT + 1)^2 z + (R - 1)(dT + 1)^2 (d + 1)^2 \neq 0$$

for $\text{Re } z \geq 0$. Straightforward calculations show that the first two Hurwitzian determinants of this fourth-order polynomial in z are positive and thus the stability criterion reduces to the question of the sign of the third Hurwitzian determinant. It turns out that the third Hurwitzian determinant is a quadratic in R which is positive for small R and which is increasing for large R . It is not worth the space here to exhibit and study this rather complicated quadratic in detail. Suffice it to say that under certain circumstances (that is, for certain choices of d and T) this quadratic will have two positive roots and hence become negative for R , or in other words b , greater than a critical value (the smaller root). This is numerically illustrated in Fig. 3 below.

We conclude that *in the absence of a significant gestation period the equilibrium birth rate can be unstable for birth moduli larger than a critical value b_0 when a maturation period is present and age-specific fecundity is affected maximally by individuals of an age $T > 0$.*

Numerically integrated examples illustrating stable and unstable cases can be seen in Fig. 3.

Although qualitatively one would expect a similar conclusion if the "reproductive window" as measured by $1/n$ in $\beta(a) = p_{n,1}(a)$ and/or the width of the peak for the weighting function $w(a, \sigma) = p_{n,T}(\sigma)$ as again measured by $1/n$ are decreased, the range of values of the parameters b, d, T under which instability is present may of course change. For example, in the limit as $n \rightarrow +\infty$ these distributions approach the Dirac functions at 1 and T respectively and the stability criterion becomes

$$1 + (R - 1)e^{-zT} - e^{-z} \neq 0 \quad \text{for } \text{Re } z \geq 0.$$

As a specific case consider $T = 1/2$. The equation $1 + (R - 1)e^{-z/2} - e^{-z} = 0$ has roots

$$z = -\ln \xi^2 - (2k + 1)2\pi i, \quad k = 0, \pm 1, \pm 2 \dots, \\ \xi = \{R - 1 - [(R - 1)^2 + 4]^{1/2}\} / 2$$

lying in the right half plane for all values of b for which $R > 1$, i.e. $b > e^d$. Thus the positive equilibrium is *always unstable* in this case, unlike the

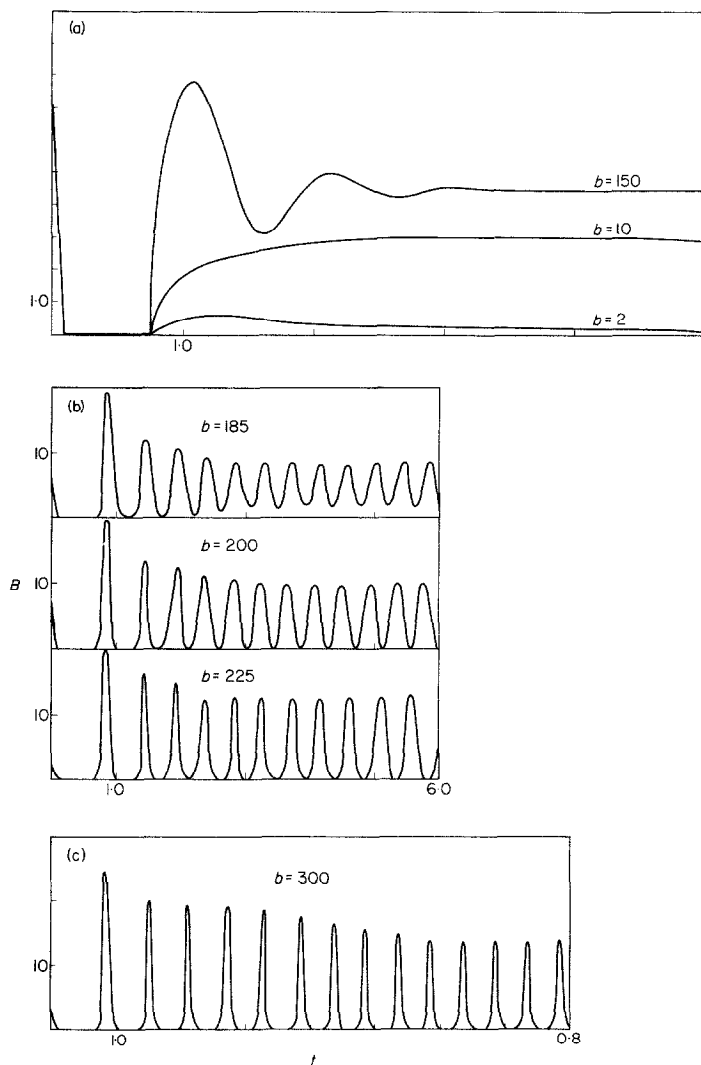


FIG. 3. Numerical solutions of equation (5) are shown for $\beta(a) = a e^{-a}$, $w(a, \sigma) = T^{-2} \sigma e^{-\sigma/T}$, $T = 1.2$ and $d = 1.0$. The equilibrium $B_{\infty} = (dT+1)^2 [b - (1+d)^2] / b = 4.84(b-4)/b$ is positive if and only if $b > 4$. In (a) when $b = 2$, $B_{\infty} < 0$ and the solution tends to zero as $t \rightarrow +\infty$. The remaining two solutions in (a) are stable and tend to B_{∞} as $t \rightarrow +\infty$, but an increase of b from 10 to 150 has resulted in the appearance of oscillations. Further increases in b result in an unstable equilibrium (and increasingly pronounced, sustained oscillations) as shown in (b). In (c) where $b = 300$ the birth rate $B(t)$ is periodically large with distinct intervening periods at zero. This figure illustrates the instability of the equilibrium when the density effects on fecundity are weighted towards an older age class and the birth modulus is large in a model equation (5) in which gestation periods are ignored.

previous case when instability occurred only for birth moduli larger than a critical value. *This example suggests that the narrowing of the age span of most active reproductivity (i.e. of the "reproductive window") and of the weighted age effects on fecundity promotes instability.*

A positive equilibrium is not always unstable in this example however. If instead we take $T=2$ then all the roots of the characteristic equation $1 + (R-1)e^{-2z} - e^{-z} = 0$ lie in the left half plane only for $b < b_0 := 2e^d$. For $b > b_0$ there are roots in the right half plane (with real parts $\frac{1}{2} \ln(R-1)$, $R = b e^{-d}$). The same is true when $T=1$ except that in this case $b_0 := 3e^d$.

Many experiments with various insect species have demonstrated equilibria and sustained oscillations and it is often age structure phenomena coupled with a high birth modulus b which is offered as an explanation for these instabilities. Slobodkin (1961) discusses at length undamped oscillations in several insect species and he offers several explanations based on delay causing mechanisms due to the age structure and the life cycle of these insects. Different species of insects can have of course quite different life cycles, but those in which the larva and adults feed on different resources [such as the blowfly *Lucilia* in the famous experiments of Nicholson (1954)] can, because of this, experience a time lag in the affect of increased density on the fecundity of adults. This explanation of observed instability of equilibria in these types of insect populations, which also have large birth modulus coefficients, is consistent with the conclusions drawn above.

On the other hand some insect species have simpler life cycles in which all animals in the population compete for food resources at all age levels. Such is the case of the water flea *Daphnia* which Slobodkin (1961) found also to exhibit undamped oscillations under certain circumstances. This case is perhaps reasonably modeled by the weighting function $w(a, \sigma) \equiv w_0 = \text{constant} > 0$ which, as in case 4.A above, implies that fecundity depends on total population size. It was shown in 4.A above, however, that such a case in the model considered here always leads to a stable equilibrium and consequently this model does not seem to explain adequately the instabilities and sustained oscillations observed by Slobodkin in his experiments. Another source of time delay and possible instability which is also present in *Daphnia* is a gestation period, as pointed out by Slobodkin. Such a delay can cause the stable models in 4.A to become unstable as will now be shown.

(C) GESTATION PERIODS

In order to illustrate the destabilizing effect of a gestation period consider the case $\beta(a) \equiv 1$, $w(a, \sigma) \equiv w_0 = \text{constant} > 0$. Thus fecundity is not age-dependent and depends on total population size. [For a further study of this

case see Cushing (1979b).] Then the equilibrium $B_\infty = d(b-d)/w_0b$ is positive when $b > d$, which is assumed true.

The characteristic function is $\Delta(z) = 1 - (2d-b)g^*(z)/(z+d)$. If the gestation probability density function is chosen to be the distribution $g(s) = p_{n,T}(s)$ given by (11), then this characteristic function becomes $\Delta(z) = 1 - (2d-b)n^{n+1}/(Tz+n)^{n+1}(z+d)$. The equilibrium is unstable if $\Delta(z)$ has roots in the right half plane. The equation $\Delta(z) = 0$ is, for $\text{Re } z \geq 0$, equivalent to the equation

$$\left(\frac{Tz+n}{n}\right)^{n+1}(z+d) - (2d-b) = 0$$

which, by standard theorems in complex analytic function theory, has a root satisfying $\text{Re } z > 0$ if the limiting (as $n \rightarrow +\infty$) equation

$$ze^{Tz} + de^{Tz} - (2d-b) = 0 \quad (12)$$

does. Applying a theorem of Hayes (Bellman & Cooke, 1963, p. 44) one finds that all roots of equation (12) satisfy $\text{Re } z < 0$ if and only if $dT < bT < 2dT + (\alpha^2 + d^2T^2)^{1/2}$ where α is the unique root of $\alpha = -dT \tan \alpha$ which satisfies $0 < \alpha < \pi$. Thus, for a sharply defined gestation period the equilibrium B_∞ is unstable for certain ranges of parameter values b , d and T . Note that as $b > 0$ is increased one sees a positive equilibrium only after b surpasses the death rate d and that this equilibrium is stable until b surpasses the larger value $2d + [(\alpha/T)^2 + d^2]^{1/2} := b_0$.

Even a broadly defined gestation period can result in instabilities. For example, if $n = 1$, i.e. if $g(s) = p_{1,T}(s)$, then the characteristic equation $1 - (2d-b)/(Tz+1)^2(z+d) = 0$ for $\text{Re } z \geq 0$ is equivalent to the cubic equation $(Tz+1)^2(z+d) + (b-2d) = 0$ which by the Hurwitz criteria has roots in the right half plane if and only if

$$b > b_0 := 2d^2T + bd + 2T^{-1}. \quad (13)$$

Thus the positive equilibrium is stable if $d < b < b_0$ and unstable if $b > b_0$. Note that in this particular model the critical value of the birth modulus b_0 increases (which may be viewed as a stabilizing effect) if the gestation period either decreases below $T = 1/d$ or increases above $T = 1/d$ and that *this critical value b_0 is minimal, or in other words the model is "most unstable", when $T = 1/d$, i.e. when the "most probable" gestation time T equals the expected lifespan of an individual female.*

This discussion shows that a gestation period can easily cause instabilities in a model which is otherwise stable. This instability causing property of a gestation period is likewise present in the other case considered in (4.A), namely when fecundity depends on the present birth rate. To see this let

$w(a, \sigma) = \delta_0(\sigma)$, $\beta(a) \equiv 1$ and $g(s) = p_{1,T}(s)$. Then again $B_\infty = (b - d)/b$ is positive only if $b > d$. The characteristic equation $\Delta(z) = 0$ is equivalent to the cubic equation

$$T^2 z^3 + T(dT + 2)z^2 + (2dT + bd^{-1})z + (b - d) = 0.$$

By means of the Hurwitz criteria one finds that B_∞ is always stable. On the other hand if the gestation period is slightly more narrowly defined in the sense that $g(s) = p_{2,T}(s)$ then the characteristic equation is equivalent for $\text{Re } z > 0$

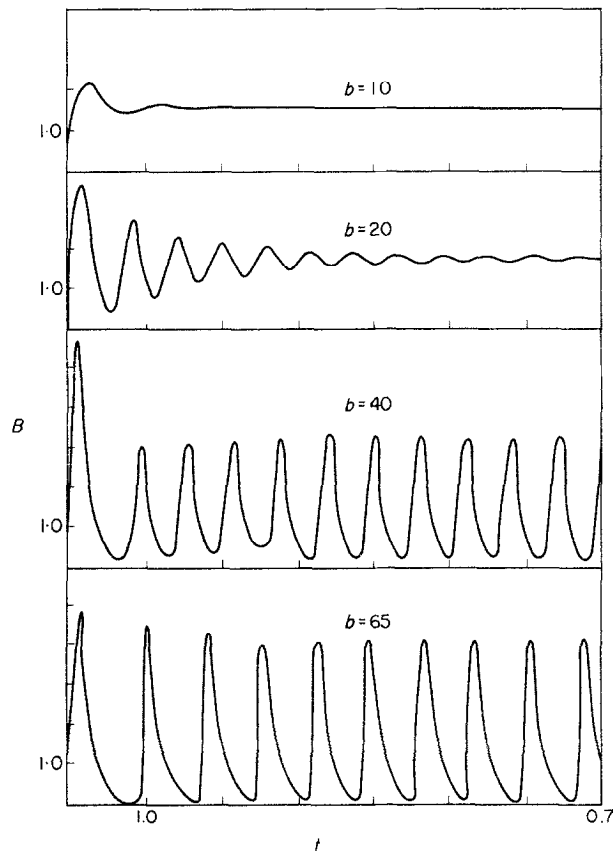


FIG. 4. Four graphs of numerically computed solutions of (5) are shown for $g(s) = T^{-2}s e^{-s/T}$, $T = 0.1$, $w(a, \sigma) \equiv 1$, $\beta(a) \equiv 1$ and $d \equiv 2$. The equilibrium $B_\infty = 2(b - 2)/b$ is stable for $b < b_0 = 32.8$ [see (13)]. Instability of B_∞ and sustained oscillations are observed for $b = 40$ and 65. This graph illustrates instabilities arising from a gestation period and a large birth modulus in equation (5).

to the quartic equation

$$T^3 z^4 + T^2(dT + 6)z^3 + 6T^2(d + 2T)z^2 + 4(3dT^3 + 2bd^{-1})z + 8(b - d) = 0$$

which, as can be shown by the Hurwitz criteria, has roots in the right half plane if b is large enough.

Thus the stable models in 4.A above can be made unstable by the inclusion of a gestation period. Also instability is promoted by a narrowing of the span of the gestation period.

This conclusion is illustrated in Fig. 4 where numerically computed solutions are not only seen to be unstable for large birth moduli, but are seen to exhibit sustained oscillations.

(D) AGE DEPENDENT WEIGHTING FUNCTIONS w

In all of the cases 4.A-C considered above the weighting function w was assumed to be independent of age a , that is to say that whereas differing age classes may have different weighted effects on fecundity, they nonetheless affect the fecundity of all age classes equally. To say that w depends on age a means that the age specific weighted effect of population density affects different age classes differently. Because the complicated way in which the weighting function w enters into the characteristic function $\Delta(z)$ makes it difficult to make any general study of this obviously interesting and biologically reasonable case, only a special case which is frequently studied in the literature will be considered here.

Suppose that the density of any age class can affect the fecundity of only its own age class (see Hoppenstaedt, 1975). That is, suppose $w(a, \sigma) = w_0 \delta_a(\sigma)$ so that $\int_0^\infty w(a, \sigma) n(t, \sigma) d\sigma = w_0 n(t, a) = w_0 B(t - a) e^{-D(a)}$ in the fecundity function (2). Thus age specific fecundity depends on the birth rate a time units ago or, in other words, an individual's fecundity is a functional of the population's total birth rate at the time of that individual's own birth only. If in addition we ignore, for simplicity, the death rate: $d = 0$, then the model equation (5) becomes

$$B(t) = \int_{-\infty}^t g(t-s) \int_{a=0}^{\infty} b\beta(a)[1 - w_0 B(s-a)]_+ B(s-a) da ds, \quad (14)$$

with positive equilibrium $B_\infty = (b-1)/w_0 b > 0$ if and only if $b > 1$. [It is assumed that $\int_0^\infty \beta(a) da = 1$.] The characteristic function of the linearization at this equilibrium is

$$\Delta(z) = 1 - (2-b)g^*(z)\beta^*(z). \quad (15)$$

In the case of no gestation period [$g^*(z) \equiv 1$] and a maturation function $\beta(a) = p_{n,T}(z)$ as given by (11), the stability condition (7) becomes

$$1 - (2 - b)n^{n+1} / (Tz + n)^{n+1} \neq 0, \quad \text{Re } z \geq 0.$$

A straightforward investigation of this condition shows that B_∞ is stable for all $b > 1$ if $n = 1$ and for $1 < b < b_0 := 2 + \sec^{n+1}[\pi/(n + 1)]$ if $n \geq 2$ while B_∞ is unstable if $n \geq 2$ and $b > b_0$.

Thus we again see the possibility of instabilities due to age specific fecundities in a population provided, in this particular case, that the birth modulus is large enough and the width of the "reproductive window" is small enough. Note that the critical value b_0 of the birth modulus in this case is independent of the age T of maximum fecundity and the constant w_0 (the reciprocal of which is the magnitude of the total birth rate at which fecundity drops to zero). The critical birth modulus b_0 decreases with the "width" $1/n$ of the reproductive window.

It is perhaps interesting to point out that if in equation (14) one lets $g(s) = \delta_{T_1}(s)$ and $\beta(a) = \delta_{T_2}(a)$, then equation (14) reduces to the equation

$$B(t) = b[1 - w_0 B(t - T_3)]B(t - T_3), \quad T_3 := T_1 + T_2$$

which, if t is sampled at discrete integer multiples of T_3 , yields the well-known difference equation

$$B_n = b(1 - w_0 B_{n-1})B_{n-1}$$

where $B_n = B(nT_3)$. Solutions of this difference equation are well known to have, depending on the value of b , an astonishingly rich set of behavioral possibilities, including what has become to be called "chaotic" behavior. Thus we obtain a hint of the possibility of the existence of such exotic solutions of the more general model equation (5).

(E) GESTATION PERIODS TOGETHER WITH AGE SPECIFIC FECUNDITY

In all of the examples considered above either it was assumed that no gestation period was present [$g(s) = \delta_0(s)$] or that the maturation function $\beta(a)$ was independent of age [$\beta(a) \equiv 1$]. In a real population of course there are undoubtedly present both a gestation period and age specific fecundity. As we have repeatedly said above anything but simpler special cases of the model equation (5) are difficult if not impossible to study in any generality. Thus in order to make one final point concerning now the interplay of these two delay causing mechanisms, a special case will be examined.

Suppose that we again consider the case discussed in 4.D, but without the assumption $g(s) = \delta_0(s)$. Thus, we assume that only age class a affects the

fecundity of age class a , that is $w(a, \sigma) = \delta_a(\sigma)$, and we ignore the death rate: $d = 0$. Suppose that we take $\beta(a) = p_{1, T_1}(a)$. Let the gestation probability density function be $g(s) = p_{1, T_2}(s)$. From the characteristic function (15) one finds, after some algebraic manipulations, that the equilibrium $B_\infty = (b-1)/b > 0$ is stable if and only if all roots of the quartic polynomial

$$(T_1 T_2)^2 z^4 + 2T_1 T_2 (T_1 + T_2) z^3 + (T_1^2 + 4T_1 T_2 + T_2^2) z^2 + 2(T_1 + T_2) z + (b-1) = 0$$

lie in the left-half plane. The Hurwitz criteria show that this occurs if and only if

$$1 < b < b_0 := (T_1/T_2) + 4 + (T_2/T_1).$$

Thus we again reach the conclusion that a large birth modulus results in instabilities.

The symmetric dependence of the critical value b_0 of the birth modulus on T_1 and T_2 can be used to draw some interesting conclusions in the case being studied here. T_1 is the "most probable" gestation time and T_2 is the age of

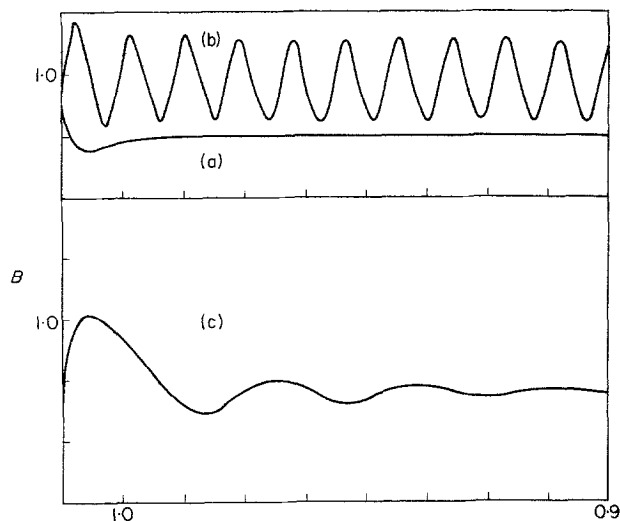


FIG. 5. Three numerically integrated solutions of equation (5) are shown for $g(s) = T_1^{-2} s e^{-s/T_1}$, $T_1 = 0.1$, $\beta(a) = T_2^{-2} a e^{-a/T_2}$, $w(a, \sigma) = \delta_a(\sigma)$ and $d = 0$. The equilibrium is $B_\infty = (b-1)/b$. (a) $b = 2.0$, $T_2 = 0.2$ shows a stable equilibrium $B_\infty = 0.5$. Because of the presence of a gestation period ($T_1 = 0.1$) the equilibrium becomes unstable when in (b) the value of the birth modulus is increased to $b = 10.0$ (with T_2 held fixed at 0.1). Graph (c) illustrates the restabilization of the equilibrium by an increase to 1.0 of the "maturation period" T_2 [with the gestation period T_1 held fixed at 0.1 and the birth modulus b held fixed at 10.0 as in the unstable case (b)].

maximum reproductivity or simply the “maturation period”. Given a birth modulus b , a decrease (increase) in the critical value b_0 can be considered a destabilizing (stabilizing) effect on the equilibrium. As a function of T_i , for fixed T_j , $j \neq i$, b_0 monotonically decreases to $b_0 = 6$ at $T_i = T_j$ and then increases with $T_i > T_j$. An increase in a *small* gestation (or a maturation) period can be viewed as destabilizing whereas an increase in a *large* gestation (or maturation) period is stabilizing.

Thus, in this example it is not accurate to say that delays caused by gestation and maturation periods are destabilizing. For example, clearly a proportional increase in both T_1 and T_2 leaves the critical value b_0 unchanged. *But more than this, the opposite can be true: an increased maturation or gestation period can stabilize an unstable equilibrium.* For example, if the gestation period T_1 is less than the maturation period T_2 but is such that $b > b_0$ so that the equilibrium is unstable, then an *increase* in the maturation period T_2 will increase b_0 and can, if increased enough, result in $b < b_0$ and hence stability. Due to the symmetry of the roles played by T_1 and T_2 in b_0 the same is true if T_1 and T_2 are interchanged. *In this sense a maturation (or gestation) period delay can stabilize what would be an otherwise unstable equilibrium, as caused by a gestation (or maturation) period and a large birth modulus.* A numerically integrated example of this phenomenon is given in Fig. 5.

5. Summary

The special cases considered in this paper are summarized in Table 1 below.

The notion of “generation time” as a crude delay causing and hence destabilizing agent in the growth dynamics of a single species consists of at least three basic components: a gestation period, age-specific fecundity rates and age-specific functional dependence of fecundity on population density. The model equation (5) for the total birth rate of an age-structured population has been used to study the effect that these three entities can have on the equation’s equilibrium.

In case 4.A it is shown that age-specific fecundities do not necessarily lead to instabilities. The simple models considered in 4.A contain no gestation delay and assume that fecundity is dependent on either total population size or the present time, total birth rate. The equilibria in 4.A are always stable for all (age dependent) maturation functions $\beta(a)$. In 4.C it is shown that these stable models can become unstable by the inclusion of a gestation period provided the birth modulus is large.

The cases in 4.B and 4.D show that the age structure alone, however, can be a source of instability. This instability is caused not only by the presence

TABLE 1

Cases considered in section 4	Death rate $d(a) \equiv d$	Gestation function $g(s)$	Maturation function $\beta(a)$	Density weighting function $w(a, \sigma)$	Net reproductive rate R	Equilibrium $B_\infty > 0$
(A) No gestation period. Fecundity depends on total population size or on total present birth rate. Arbitrary maturation function.	$d \geq 0$	$\delta_0(s)$	Arbitrary	$w_0 \equiv \text{constant}$ or $w_0 \delta_0(\sigma)$	$b\beta^*(d)$	Stable for all birth moduli b .
(B) No gestation period. Fecundity depends mostly on density of individuals of age $T > 0$. Maturation period equals one time unit.	$d \geq 0$	$\delta_0(s)$	$p_{1,1}(a)$ or $\delta_1(a)$	$p_{1,T}(\sigma)$ or $\delta_T(\sigma)$	$b/(1+d)^2$ or $b e^{-d}$	Loss of stability at a critical value b_0 of the birth modulus b . or Instability for all birth moduli b .

<p>(C) Gestation period $T > 0$. No age dependence in vital parameters. Fecundity depends on total population size. Maturation function is age independent.</p>	<p>$d > 0$</p>	<p>$p_{n,T}(s)$ $1 \leq n \leq +\infty$</p>	<p>1</p>	<p>$w_0 = \text{constant}$</p>	<p>b/d</p>	<p>Loss of stability at a critical value b_0 of the birth modulus b.</p>
<p>(D) No gestation period. Fecundity depends on total birth rate at time of birth. Maturation period $T > 0$.</p>	<p>$d = 0$</p>	<p>$\delta_0(s)$</p>	<p>$p_{n,T}(a)$</p>	<p>$w_0 \delta_a(\sigma)$</p>	<p>b</p>	<p>Loss of stability at a critical value b_0 of the birth modulus b.</p>
<p>(E) Gestation period $T_2 > 0$. Fecundity depends on total birth rate at time of birth. Maturation period $T_1 > 0$.</p>	<p>$d = 0$</p>	<p>$p_{1,T_2}(s)$</p>	<p>$p_{1,T_1}(a)$</p>	<p>$\delta_a(\sigma)$</p>	<p>b</p>	<p>Loss of stability at a critical value b_0 of the birth modulus b.</p>

of a age-dependent maturation function $\beta(a)$, but by the nature of the dependence of fecundity on population density. In case 4.B fecundity depends on a weighted functional of density which is heavily weighted towards an old enough age class. In 4.D fecundity depends on the total birth rate at the time of an individual's birth.

In the final case 4.E a simple case of equation (5) is considered in which both a gestation and maturation period are present. While instabilities can be present for appropriate values of the parameters, it is not true that large gestation and/or maturation periods imply instability. Moreover, in this example, an unstable equilibrium can be stabilized under certain circumstances by an increase of either period.

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