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Oscillations in age-structured population models with an Allee effect

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Abstract

A nonautonomous ordinary differential delay equation for the birth rate of a model age-structured population is derived under the assumptions that nonlinear density effects on fertility exhibit an “Allee effect”. It is shown how this assumption produces an interval of inherent net reproductive numbers less than one on which there exist two stable (asymptotic) equilibria. Furthermore, in the presence of a maturation delay and a sufficiently narrow age-specific fertility window, numerical solutions show that a certain type of attracting, large amplitude “synchronous” oscillation can also exist on this interval. A heuristic argument is given for the existence of such oscillations using the model obtained when the length of the fertility window shrinks to zero.

Keywords: Allee effect; Maturation delays; Synchronous oscillations; Delay differential equations

1. Introduction

In autonomous models of single-species population dynamics oscillations in population densities are most commonly attributed to growth rate delays in response to changes in population density. If asymptotic dynamics are studied as a function of some model parameter that measures population fertility (such as the “inherent net reproductive number”; see below), the usual scenario is as follows. The population goes extinct until the parameter is increased beyond a critical value, after which the population survives by equilibrating to a positive equilibrium level. Mathematically, a transcritical bifurcation of equilibrium branches occurs at the critical value of the parameter and there is an exchange of stability between the zero (extinction) equilibrium and the positive equilibrium on the bifurcating branch. As the parame-

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ter is further increased, the stable positive equilibrium can, in the presence of a time delay, in turn lose stability as a Hopf bifurcation occurs and small-amplitude periodic oscillations arise around the positive equilibrium. For example, see [11].

In the above scenario the model equations are nonlinear because of “density dependence”, i.e., the assumption that fertility and survival rates are affected by population density. The usual assumption is that these density effects are deleterious and consequently that fertility and survival rates decrease as population density increases. It is under these assumptions that the above described scenario takes place.

It is well-documented, however, that the adverse effects of increased population density on both fertility and survival may hold only for large population densities and that, in fact, at small densities increased population density can be advantageous. See [2] for an extensive early discussion of this phenomenon. This “Allee effect” has been observed, for example, in beetles, starfish, protozoa, shrimp, grasshoppers, *Drosophila* and waterfleas [2], paramecium [14], rotifers [13], various species of insects [18], pines [17], and annual plants [16]. The “Allee effect” has also been called the “allelocatalytic effect” [15] and “strict depensation” [4].

Our purpose here is to show that the combination of an Allee effect and a time delay can cause a certain type of oscillation to occur in model populations, an oscillation of an entirely different type from the small-amplitude oscillations that arise from a Hopf bifurcation. These oscillations occur suddenly as *large* amplitude oscillations when the inherent net reproductive number increases through a critical value (less than one). Moreover, they have the property that age cohorts are “synchronized”, i.e., at any given time certain age cohorts are entirely missing and hence the population consists of individuals from only distinct age classes. These kinds of oscillations were first observed in simple discrete population models by the author [5] and were later studied in certain kinds of age-structured models [1].

In this paper the occurrence of these “synchronized” oscillations will be studied in a model population with an Allee effect and a delay due to an age-specific maturation period. The model is described in Section 2 and shown to lead to a nonautonomous differential delay equation. It is also shown in Section 2 how the Allee assumption leads to a subcritical bifurcation of “asymptotic” equilibria and consequently to an interval of inherent net reproductive numbers less than one on which there exist two stable “asymptotic” equilibria, the positive state and the zero state. In Section 3 evidence for “synchronized” oscillations is given by means of numerical solutions when the age-specific fertility window is sufficiently narrow. A heuristic argument is given for the existence of these oscillations using the model equation obtained by letting the fertility window shrink to a single-age class.

2. An age-structured model with Allee effect

In the age-structured model considered here it will be assumed that only adult fertility is age- and density-dependent and that the death rate of all individuals is a constant $\delta > 0$. The total population birth rate $b(t)$ at time $t \geq 0$ is the sum of the total birth rate $x(t)$ of all those individuals who were born after the initial time $t = 0$ and the total birth rate $b_0(t)$ of all those individuals who were initially present at time $t = 0$ so that

$$b(t) = b_0(t) + x(t), \quad t \geq 0. \quad (2.1)$$

Let r denote the “inherent net reproductive number”, i.e., the expected number of offspring per individual per lifetime in the absence of density effects. Denote the inherent birth rate of an individual of age $a \geq 0$, that is to say, the number of offspring produced (per unit time) in the absence of density effects, by $r\phi(a)$ where ϕ is a nonnegative function normalized so that

$$\int_0^{+\infty} \phi(a)\exp(-\delta a) da = 1, \tag{2.2}$$

so that the formula $\int_0^{+\infty} r\phi(a)\exp(-\delta a) da$ for the inherent net reproductive number correctly equals r .

The number of individuals of age a at time $t \geq a$ equals the number of individuals born $t - a$ units ago, $b(t - a) da$, multiplied times the probability $\exp(-\delta a)$ of surviving to age a . The number of offspring contributed by these individuals at time t is $r\phi(a)b(t - a)\exp(-\delta a) da$. Suppose, however, that fertility is affected by population density so that the number of offspring is instead $r\phi(a)f(b(t - a))\exp(-\delta a) da$ where the density-dependent factor f now accounts for this effect. Specifically, it is assumed in this paper that the fertility of every adult individual is affected by the total population birth rate at the time of that individual’s birth. This kind of density-dependent fertility is called the “Easterlin hypothesis” [7–9]. Thus $f = f(b(t - a))$ and

$$x(t) = \int_0^t r\phi(a)f(b(t - a))b(t - a)\exp(-\delta a) da. \tag{2.3}$$

Consider a population in which individuals become reproductive mature only after reaching a maturation age $a = m$, after which fertility is a monotonically decreasing function of age. To model this kind of age-specific fertility, the normalized age-specific birth rate ϕ is written as

$$\phi(a) = \alpha H(a - m)\exp(-\beta a), \quad \alpha > 0, \beta > 0, \tag{2.4}$$

where $H(x)$ is the Heaviside function and $\alpha\gamma^{-1}\exp(-\delta m) = 1$, $\gamma = \beta + \delta > 0$, by (2.2). With this ϕ , (2.3) yields

$$x(t) = \begin{cases} 0, & \text{for } 0 \leq t \leq m, \\ r\alpha \int_m^t f(b(t - a))b(t - a)\exp(-\gamma a) da, & \text{for } t > m. \end{cases}$$

Eq. (2.3) now becomes a nonlinear Volterra integral equation (with delay) for the total birth rate $b(t)$. However, a differential delay equation can be derived for $x(t)$ by differentiating

$$x(t) = \begin{cases} 0, & \text{for } 0 \leq t \leq m, \\ r\alpha \int_0^{t-m} f(b(a))b(a)\exp(-\gamma(t - a)) da, & \text{for } t > m, \end{cases}$$

to obtain $x'(t) = -\gamma x(t) + r\alpha e^{-\gamma m} f(b(t - m))b(t - m)$ for $t > m$ or, by (2.1),

$$x'(t) = -\gamma x(t) + r\alpha e^{-\gamma m} f(b_0(t - m) + x(t - m))(b_0(t - m) + x(t - m)), \quad t > m. \tag{2.5}$$

This equation together with the initial condition $x(t) = 0$ for $0 \leq t \leq m$ and a prescription of the total birth rate $b_0(t)$ of the initial population determine $x(t)$ for $t > m$, which in turn, by (2.1), determines the total birth rate $b(t)$.

Because the probability of living a finite length of time t decreases exponentially with rate δ in our model, it is reasonable to assume that $b_0(t)$ decreases to 0 as $t \rightarrow +\infty$ at this same rate.

Finally, something must be said about the density-dependent term $f(z)$. Because $\phi(a)$ is the inherent fertility rate (at low, or technically zero population density), it is required that $f(0) = 1$. As discussed in the Introduction, it is generally accepted that density effects are deleterious, at least at high population densities, but that at low population densities the reverse (Allee) effect is present in many species. To qualitatively capture these features, it is assumed that

$$f(0) = 1, \quad f(z) > 0, \quad \text{for } z > 0, \quad f(+\infty) = 0, \quad f'(0) > 0. \quad (2.6)$$

Thus $f(z) > 1$ at least for small $z > 0$, but $f(z) < 1$ for large $z > 0$.

From the normalization (2.2) follows

$$\alpha\gamma^{-1}\exp(-\gamma m) = 1, \quad \gamma = \beta + \delta, \quad (2.7)$$

which when substituted into (2.5) yields the equation

$$\begin{aligned} x'(t) &= \gamma(-x(t) + rf(b_0(t-m) + x(t-m))(b_0(t-m) + x(t-m))), \quad t > m, \\ x(t) &= 0, \quad 0 \leq t \leq m, \end{aligned} \quad (2.8)$$

for the birth rate $x(t)$.

In (2.8), $b_0(t)$ is a nonnegative, continuous function that decreases to 0 as $t \rightarrow +\infty$. The “limiting equation” is the autonomous differential delay equation

$$y'(t) = \gamma(-y(t) + rf(y(t-m))y(t-m)), \quad t > m. \quad (2.9)$$

Besides the trivial equilibrium $y = 0$, this equation has positive equilibria $y = e > 0$ defined by the equation $f(e) = 1/r$. The assumptions (2.6) made on $f(z)$ imply the existence of at least one positive equilibrium for $r > 1$ and at least two positive equilibria for $r_{\text{cr}} < r < 1$ where

$$r_{\text{cr}}^{-1} = \max_{z \geq 0} |f(z)|$$

(see Fig. 1).

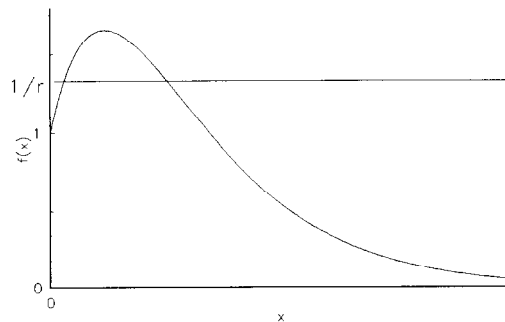


Fig. 1. A density-dependence factor $f(x)$ satisfying $f'(0) > 0$ in recognition of an Allee effect (as in assumptions (2.6)) implies the existence of two positive solutions of the limiting equilibrium equation $f(e) = 1/r$ for values of the inherent net reproductive number r less than one.

In Section 3 a special kind of oscillation will be studied for $r < 1$. First we observe that there are asymptotically constant solutions of (2.8). Given an equilibrium $e \geq 0$ of the limiting equation (2.9), define

$$b_0^e(t) = e \left(1 - \int_0^t \phi(a) \exp(-\delta a) da \right).$$

Note that $b_0^e(t) \rightarrow 0$ as $t \rightarrow +\infty$ follows from the normalization (2.2) of ϕ . It is not difficult to show that the solution of (2.8) for $t > m$ with $b_0(t) = b_0^e(t)$ is

$$x_e(t) = e \int_0^t \phi(a) \exp(-\delta a) da, \quad t > m, \tag{2.10}$$

and that by (2.2), $x_e(t) \rightarrow e$ as $t \rightarrow +\infty$, i.e., $x_e(t)$ is an asymptotically constant solution of (2.8). Let $|b|_0 = \sup_{t \geq 0} |b(t)|$. We will say that an equilibrium $y = e > 0$ of the limiting equation (2.9) is *stable* if for any $\epsilon > 0$ there exists a $\delta > 0$ such that $|b_0 - b_0^e|_0 < \epsilon$ implies that $x(t) \rightarrow e$ as $t \rightarrow +\infty$. If, however, there exist $b_0(t)$ arbitrarily close to $b_0^e(t)$ (with respect to the sup norm $|\cdot|_0$) for which the solution of (2.8) does not approach e as $t \rightarrow +\infty$, then $y = e$ will be called *unstable*. The following theorem is proved in the Appendix.

Theorem. *Corresponding to each equilibrium $y = e \geq 0$ of the limiting equation (2.9) there is at least one solution of (2.8) asymptotic to e as $t \rightarrow +\infty$. If $r < 1$, then $e = 0$ is stable, and if $r > 1$, then $e = 0$ is unstable. If $e > 0$ is a positive equilibrium of (2.9), then it is stable if $f'(e) < 0$ and unstable if $f'(e) > 0$.*

For example, with an $f(z)$ as in Fig. 1, Eq. (2.8) has two “stable asymptotic equilibria” $e = 0$ and $e = e_2 > 0$, and one “unstable asymptotic equilibrium”, $e_1 > 0$.

3. Oscillations

We are interested in this paper in the possibility of a certain type of oscillatory solution of (2.8) under the Allee assumption (2.6) on the density-dependence factor $f(z)$. As r is increased through the critical value $r_{cr} < 1$, there will suddenly occur, according to the Theorem above and assumption (2.6), a positive asymptotic equilibrium of “large” amplitude which will coexist with stable state $e = 0$, at least so long as r remains less than 1; cf. Fig. 2. The type of oscillation sought is one in which the birth rate $x(t)$ rapidly changes periodically between $x = 0$ and the other stable positive equilibrium state. We will refer to these oscillations as “synchronized” because they imply that at any time only certain age cohorts are present, alternating with entirely empty age cohorts. This can be seen from the formula $b(t - a) \exp(-\delta a) \equiv x(t - a) \exp(-\delta a)$ for the density of age class a at large time t (cf. [10]).

Although we will give no rigorous proof, we will give some numerical evidence that such kinds of oscillations can asymptotically occur if the fertility period is “sufficiently narrow”, i.e., if β is sufficiently large. A heuristic motivation for these oscillations can be obtained from the limiting equation (2.9) by rewriting it as the singularly perturbed equation

$$\epsilon x'(t) = -x(t) + rf(x(t - m))x(t - m), \quad t > m,$$

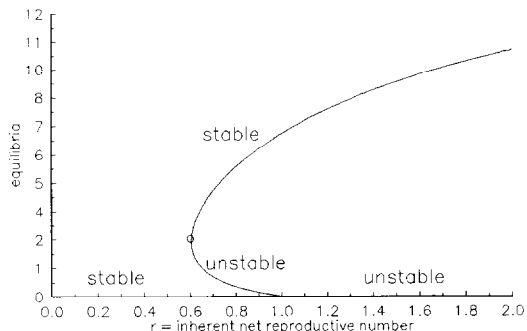


Fig. 2. In the presence of an Allee effect (i.e., assumptions (2.6) on the density-dependence factor $f(x)$), the limiting equation has a branch of positive equilibria which bifurcates “subcritically” from $e = 0$ at $r = 1$, but which turns around at a critical value $r_{cr} < 1$ where the larger stable equilibrium branch meets the smaller unstable equilibrium branch.

and setting $\epsilon = 1/\gamma = 1/(\beta + \delta) = 0$ (corresponding to $\beta = +\infty$). This yields the functional difference equation

$$x(t) = rf(x(t - m))x(t - m), \quad t > m. \tag{3.1}$$

Consider an $f(z)$ whose graph appears as in Fig. 1 for which the graph of $f(z)z$ appears as in Fig. 3. In this case there are two positive equilibria $0 < e_1 < e_2$. Let $x_0(t) \geq 0$ denote a given initial function defined on $[0, m]$. If $t_0 \in [0, m]$ is such that $z_0 = x_0(t_0) \in [0, e_1)$, then the sequence defined by $z_i = z(t_i)$ for $t_i = t_0 + im, i = 0, 1, 2, \dots$, which satisfies $z_{i+1} = rf(z_i)z_i$, will tend to 0 as $t \rightarrow +\infty$, while the same sequence will tend to e_2 if $z_0 > e_1$ (see Fig. 3). Thus

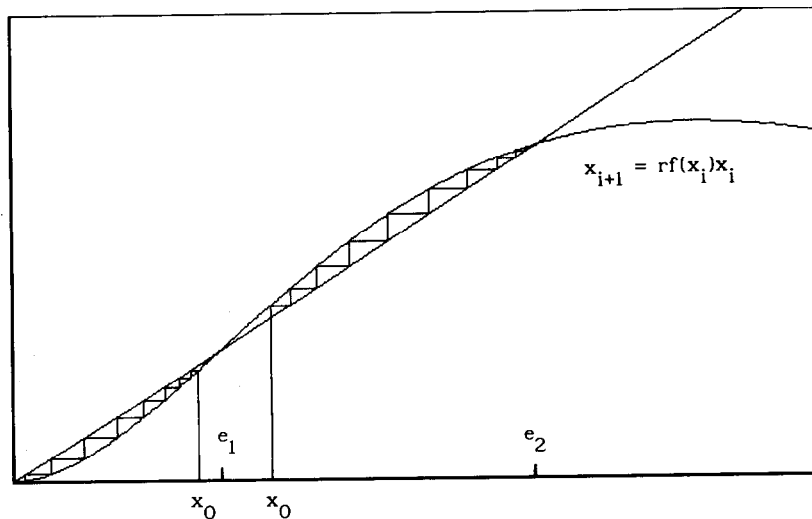


Fig. 3. The “cobweb” diagram for the difference equation $x_{i+1} = rf(x_i)x_i$ when $r_{cr} < r < 1$ shows how initial $x_0 > 0$ that are smaller than the unstable equilibrium e_1 lead to sequences tending to zero, while those larger than e_1 lead to sequences tending to the larger positive equilibrium e_2 .

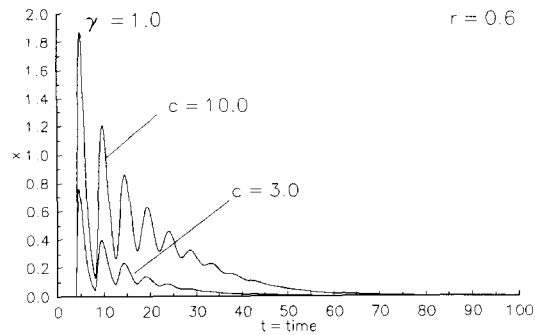


Fig. 4. The graphs of two solutions of (2.8) with (3.2) and (3.3) are shown when $r = 0.6 < r_{cr} \approx 0.64$. This illustrates that the model population goes extinct when $r < r_{cr}$. Parameters values used were $m = 4$, $\delta = 2$, $\gamma = 1$, $a = 1$, $b = 0.3$.

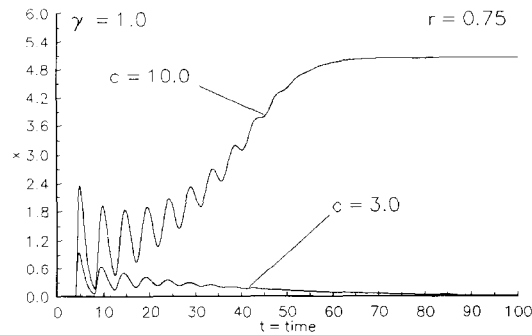


Fig. 5. The graphs of two solutions of (2.8) with (3.2) and (3.3) are shown when the model parameter values are the same as in Fig. 4 except that r has been increased to $r = 0.75 > r_{cr} \approx 0.64$. As predicted by the Theorem, there are two attracting asymptotic equilibrium states, $e = 0$ and $e_2 \approx 5.1 > 0$, when $r < 1$ exceeds r_{cr} .

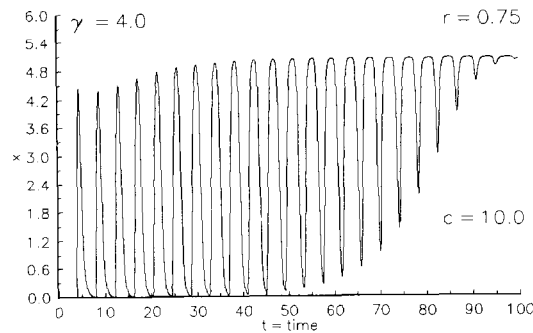


Fig. 6. The effect of increasing γ (from 1 to 4) on one of the solutions in Fig. 5 (the one corresponding to $c = 10$) can be seen by its graph. The solution still equilibrates to the positive equilibrium $e_2 \approx 5.1$, but initially suffers large amplitude oscillations in which the solution drops very near zero for over ten model generations (a generation is $m = 4$ time units).

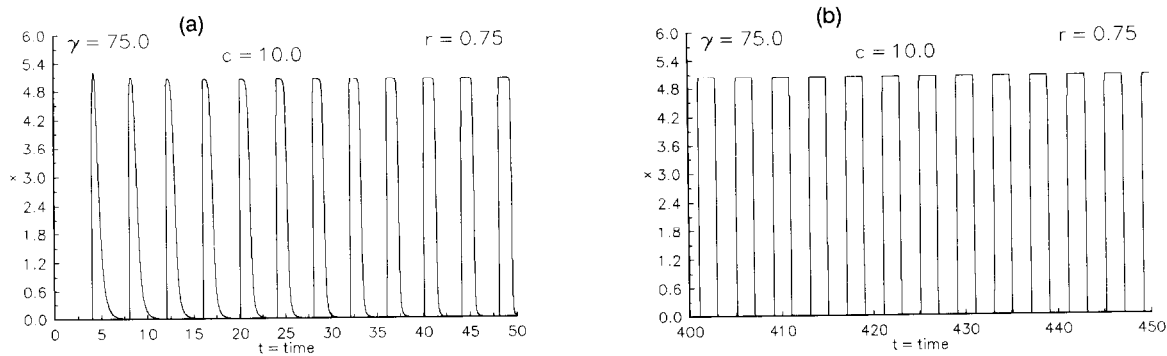


Fig. 7. The effect of further increasing γ (to 75) on the solution in Fig. 6 is seen by its graph. After some transient oscillations shown in Fig. 7(a), the solution apparently settles into a “square wave” type of periodicity shown in Fig. 7(b) in which the solution alternates between 0 and the positive equilibrium $e_2 \cong 5.1$. In this example the oscillation has persisted for over 100 model generations, although we have no mathematical proof that the solution has stabilized on this periodicity for all $t > 0$.

the solution of (3.1) will resemble for large t a discontinuous function of period m which equals 0 on the set $\{t \in [0, m]: x_0(t) < e_1\}$, equals e_2 on $\{t \in [0, m]: x_0(t) > e_1\}$, and equals e_1 on $\{t \in [0, m]: x_0(t) = e_1\}$.

A simple function that satisfies all of the above conditions is

$$f(z) = (1 + az)\exp(-bz), \quad a > b > 0. \quad (3.2)$$

Solutions of the delay equation (2.8) were numerically calculated with initial birth rates of the form

$$b_0(t) = c \exp(-\delta t), \quad c > 0. \quad (3.3)$$

In Fig. 4 we see examples of solutions that tend to 0 because $r < r_{rc} = ba^{-1}\exp((a-b)/a)$, while in Fig. 5 we clearly see the two asymptotically constant solutions guaranteed by the Theorem when $r_{cr} < r < 1$, namely $x = 0$ and $e_2 > 0$. The solutions in Figs. 4 and 5 are for “small” γ . As γ is increased, the asymptotically constant solution tending to e_2 begins to exhibit large-amplitude oscillations between small values near $x = 0$ and larger values near e_2 ; see Fig. 6. For the “large” γ in Figs. 7(a) and 7(b) we see oscillations which are persistent for over 100 generations. Extensive simulations show that in order to obtain such long-term synchronous oscillations the initial birth rate $b_0(t)$ must assume both sufficiently small and sufficiently large values, that β (specifically γ) must be sufficiently large, and r must lie in the interval $(r_{cr}, 1)$ guaranteed by the Allee condition.

4. Concluding remarks

We have investigated a model population whose density-dependent fertility rate exhibits an Allee effect, i.e., a fertility rate that *increases* when *low*-level population densities are increased, but decreases when *high*-level population densities are increased. It was shown how this assumption implies a subcritical bifurcation of asymptotic, positive equilibria as the

inherent net reproductive number r of the population is increased. This in turn implies the existence of an interval $(r_{cr}, 1)$ of r values on which the model population has two stable asymptotic equilibria, one positive and one identically zero.

The main conclusion to be drawn here is that when these biological features are coupled with an age-specific maturation period and a sufficiently narrow age-specific fertility window, there can exist asymptotic synchronous oscillations, in addition to the stable asymptotic equilibria, on the interval $(r_{cr}, 1)$. This is shown by means of numerical simulations and a heuristic argument based upon the model equations (2.8) and (2.9). “Synchronous” oscillations are oscillations in time in which the birth rate rapidly alternates between intervals on which it equals the stable positive equilibrium and intervals on which it equals zero. These oscillations give rise to population densities in which age cohorts are entirely missing, i.e., in which individuals appear in synchronized age classes.

We have, however, no mathematical proof of the existence nor the stability of these synchronous oscillations for the delay equation (2.8).

Appendix

Proof of the Theorem. The first sentence is proved by $x(t)$ given by (2.10). Consider now the trivial equation $e = 0$ of the limiting equation (2.9). By (2.1) and (2.3) the total population birth rate $b(t)$ satisfies the Volterra integral equation

$$b(t) = b_0(t) + \int_0^t r\phi(a)f(b(t-a))b(t-a)\exp(-\delta a) da. \tag{A.1}$$

The linearization of this equation at $b(t) = 0$ yields

$$b(t) = b_0(t) + \int_0^t r\phi(a)b(t-a)\exp(-\delta a) da.$$

The characteristic equation associated with this linear equation is

$$1 - \int_0^{+\infty} r\phi(a)\exp(-(\delta + z)a) da = 0, \tag{A.2}$$

which can, using (2.4), be rewritten as $-\gamma \exp(mz) + r\gamma - z \exp(mz) = 0$ or, with $\zeta = mz$, as $-\gamma \exp(\zeta) + r\gamma - m^{-1}\zeta \exp(\zeta) = 0$. Hayes Theorem [3] applied to this last equation shows that (A.2) has no roots with $\text{Re}(z) \geq 0$ if and only if $r < 1$. Suppose first that $r < 1$. [12, Theorem 2] implies that there exists an $\epsilon > 0$ such that $|b_0|_0 < \epsilon$ implies $b(t) \rightarrow 0$ as $t \rightarrow +\infty$. Inasmuch as $b_0(t) \rightarrow 0$ implies $x(t) = b(t) - b_0(t) \rightarrow 0$ as $t \rightarrow +\infty$, we have proved that $e = 0$ is stable if $r < 1$. If $r > 1$, the instability of $e = 0$ follows from [6, Corollary 4.3].

In a similar fashion, it can be shown that the linearization of (A.1) at a positive equilibrium $e > 0$ of the limiting equation (2.9) has characteristic equation

$$1 - \Delta \int_0^{+\infty} r\phi(a)\exp(-(\delta + z)a) da = 0,$$

where $\Delta = f(e) + ef'(e)$. A calculation of the integral and a rewriting as above leads to the equation $-\gamma \exp(\zeta) + \Delta r\gamma - m^{-1}\zeta \exp(\zeta) = 0$. An application of Hayes Theorem shows that

there are no roots of this equation satisfying $\operatorname{Re}(z) \geq 0$ if and only if $r\Delta < 1$, i.e., if and only if $f'(e) < 0$. [12, Theorem 2] and [6, Corollary 4.3] now imply the last sentence of the Theorem. \square

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