STOCHASTIC POPULATION MODELS (SPRING 2015)

STEFAN GERITZ & FENGYING WEI

3. Delay differential equations

3.1. **Example.** Consider the mechanism underlying the logistic equation as presented in section 1.8. But now we distinguish between adult (X) and juvenile (Y) individuals and the following processes:

$$
\begin{array}{rcll}
\mathrm{X} & \xrightarrow{\beta} & \mathrm{X}+\mathrm{Y} & \text{(birth)} \\
\mathrm{X}+\mathrm{X} & \xrightarrow{\gamma} & \mathrm{X}+\dagger & \text{(interference competition)} \\
\mathrm{X} & \xrightarrow{\delta} & \dagger & \text{(death of an adult)} \\
\mathrm{Y} & \xrightarrow{\alpha} & \dagger & \text{(death of a juvenile)} \\
\mathrm{Y} & \xRightarrow{\varphi} & \mathrm{X} & \text{(maturation)}
\end{array}
\tag{1}
$$

The arrow representing the transition from juvenile to adult is of a different kind than the other arrows. We do this to indicate that we will not use mass-action to model maturation but instead use a *developmental delay.* The probability distribution of the length of the juvenile period among the surviving juveniles that are just turning into adults is given by the probability density φ. Or, in other words, φ is the conditional probability density of the length of the juvenile period, given survival till maturation. The probability of a newborn reaching adulthood depends on the length of the juvenile period. With a constant death rate α, the unconditional probability of a newborn eventually becoming adult is

$$\int_0^\infty \varphi(\tau)e^{-\alpha\tau}d\tau \tag{2}$$

and with a constant *per capita* birth rate β, the rate at which new adults are entering to the population at time t is

$$\int_0^\infty \beta x(t-\tau)\varphi(\tau)e^{-\alpha\tau}d\tau \tag{3}$$

where $x(t-\tau)$ is the population density at time $t-\tau$. The population equation then becomes

$$\frac{dx(t)}{dt} = \int_0^\infty \beta x(t-\tau)\varphi(\tau)e^{-\alpha\tau}d\tau - \delta x(t) - \frac{\gamma}{2}x(t)^2 \tag{4}$$

The above equation is an example of a *delay differential equation* (DDE). Because the delay is not of fixed length but distributed according to probability density φ, we talk about a DDE with a distributed delay.

As special case, assume that the developmental delay has a fixed length τ_0, i.e., $\varphi(\tau) = \delta_D(\tau - \tau_0)$ is the Dirac-delta distribution, i.e., a probability "density" with all probability mass concentrated at $\tau = \tau_0$. The population equation now becomes

$$\frac{dx}{dt} = \beta e^{-\alpha\tau_0} x_{\tau_0} - \delta x - \frac{1}{2}\gamma x^2 \tag{5}$$

where

$$x_{\tau_0}(t) = x(t - \tau_0). \tag{6}$$

Note that for $\tau_0 \to 0$ we retrieve the logistic equation as in section 1.8.

3.2. **Fixed delays.** Consider the general DDE

$$\frac{dx}{dt} = f(x, x_\tau) \tag{7}$$

for a single fixed delay $\tau > 0$. An equilibrium is defined as a constant solution $x(t) = \bar{x}$, i.e., a solution such that

$$0 = f(\bar{x}, \bar{x}) \tag{8}$$

While the stability of an equilibrium of a single ODE can be established graphically, this is not possible here. Instead we use a technique called local stability analysis. To that end, let $u = x - \bar{x}$ and $u_\tau = x_\tau - \bar{x}$ denote perturbations from the equilibrium. As a linear approximation of the DDE for small perturbations we have

$$\frac{du}{dt} = au + bu_\tau \tag{9}$$

where

$$a = \partial_x f(\bar{x}, \bar{x}) \quad \text{and} \quad b = \partial_{x_\tau} f(\bar{x}, \bar{x}) \tag{10}$$

The equilibrium $x = \bar{x}$ in the original equation corresponds to the equilibrium $u = 0$ in the linear approximation.

Substitution of the "trial solution" $u(t) = e^{\lambda t}$ into the linear DDE (9) gives

$$\lambda = a + be^{-\lambda\tau} \tag{11}$$

This is the characteristic equation of the linear DDE, and λ is an eigenvalue. The rationale behind using this "trial solution" is that we can write the general solution to the linear DDE as a linear combination of functions of this form but with different values of λ all satisfying the characteristic equation.

Writing $\lambda = \mu + i\nu$ for $\mu, \nu \in \mathbb{R}$ and splitting the real and imaginary parts of the characteristic equation and multiplication by τ gives us an equivalent but more useful representation

$$\begin{aligned} \mu\tau &= a\tau + b\tau e^{-\mu\tau}\cos(\nu\tau) \\ \nu\tau &= \quad - b\tau e^{-\mu\tau}\sin(\nu\tau) \end{aligned} \tag{12}$$

Our first task is to find for which combinations $(a\tau, b\tau)$ the equilibrium $u = 0$ is stable and for which it is unstable.

The equilibrium $u = 0$ is stable if *all* eigenvalues have a negative real part (i.e., $\mu < 0$ for all λ), and the equilibrium is unstable if *at least one* eigenvalue has a positive real part (i.e., $\mu > 0$ for at least one λ).

Instead of fixing $(a\tau, b\tau)$ and then checking whether the corresponding eigenvalues have positive or negative real parts, we turn the problem around by substituting $\mu = 0$ into the characteristic equation and solving for $(a\tau, b\tau)$ to find the boundary between the regions of stability and instability in the $(a\tau, b\tau)$-plane.

The stability boundary:

Substitution of $\mu = 0$ and $\omega \neq 0$ into the characteristic equation (12) and solving for $(a\tau, b\tau)$ gives

$$\begin{aligned} a\tau &= \frac{\nu\tau}{\tan(\nu\tau)} \\ b\tau &= \frac{-\nu\tau}{\sin(\nu\tau)} \end{aligned} \tag{13}$$

By varying $\nu\tau$ we get different values of $(a\tau, b\tau)$ tracing out curves in the $(a\tau, b\tau)$-plane as shown in Figure 1. Each of these curves corresponds to a pair of complex eigenvalues lying exactly on the imaginary axis. Crossing one of these curves in the $(a\tau, b\tau)$-plane corresponds to a pair of *complex* eigenvalues crossing the imaginary axis.

Substitution of $\mu = 0$ and $\nu = 0$ into the characteristic equation (12) and solving for $(a\tau, b\tau)$ gives

$$a\tau + b\tau = 0 \tag{14}$$

which gives an additional line in the $(a\tau, b\tau)$-plane corresponding to the existence of a *real* eigenvalue equal to zero (dashed bold line in Figure 1).

Which of the regions in the figure correspond to all eigenvalues having negative real parts or at least one eigenvalue having a positive real part? To answer that question, take $(a\tau, b\tau) = (-1, 0)$ and solve the characteristic equation for λ. This gives the unique solution $\lambda = -1$, i.e., all eigenvalues (there is only one for this case!) have a negative real part, and so the reference point $(-1, 0)$ is inside the stable region. The first crossing of the imaginary axis happens at the dashed bold line in Figure 1 or at the solid bold curve emanating from the point $(a\tau, b\tau) =$

FIGURE 1. Values of $(a\tau, b\tau)$ for which there exists a pair of complex eigenvalues exactly on the imaginary axis (solid bold lines) or for which there exists a real eigenvalue equal to zero (dashed bold line). The point $(1, -1)$ is indicated with a solid circle.

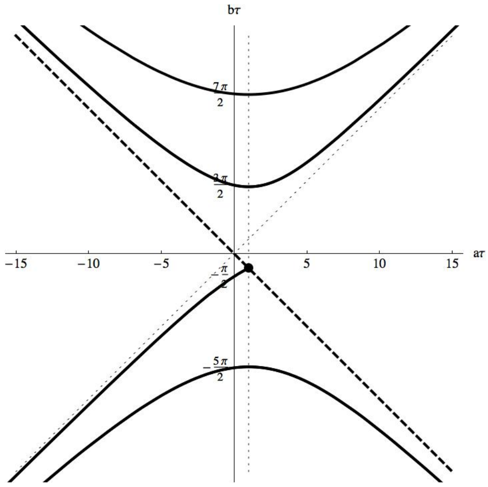
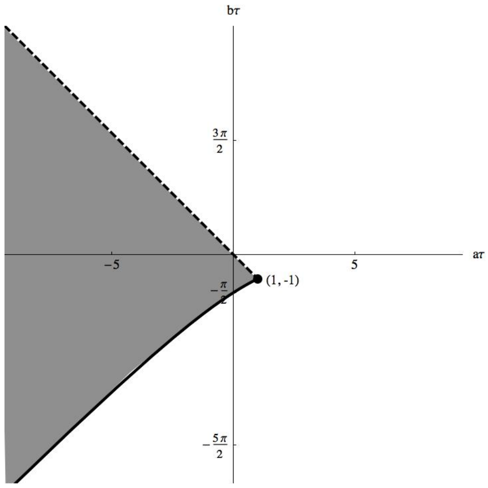


FIGURE 2. For values of $(a\tau, b\tau)$ inside the grey region the equilibrium $u = 0$ is stable, whereas outside it is unstable. Stability is lost when we cross the solid line (where a pair of complex eigenvalues crosses the imaginary axis from the left to the right) or the dashed line (where a real-valued eigenvalue crosses zero from the left to the right).



$(1, -1)$. The space in between these two lines hence corresponds to the stability region (Figure 2)

Overdamped and underdamped:

For values of $(a\tau, b\tau)$ inside the stability region, the solution of the linear DDE (9) converges monotonically to zero (the so-called *overdamped case*) if there exists a real-valued eigenvalue. But if all eigenvalues are complex, then convergence will be in an oscilatory fashion (the so-called *underdamped case*). For the filter characteristics of the system this will turn out to be an important distinction.

To find out for which $(a\tau, b\tau)$ there exist real eigenvalues, substitute $\omega\tau = 0$ into the characteristic equation (12), which gives, after a minor rearrangement,

$$a\tau = \mu\tau - b\tau e^{-\mu\tau} \tag{15}$$

Figure 3 gives the graph of $a\tau$ as a function of $\mu\tau$ for fixed value of $b\tau$.

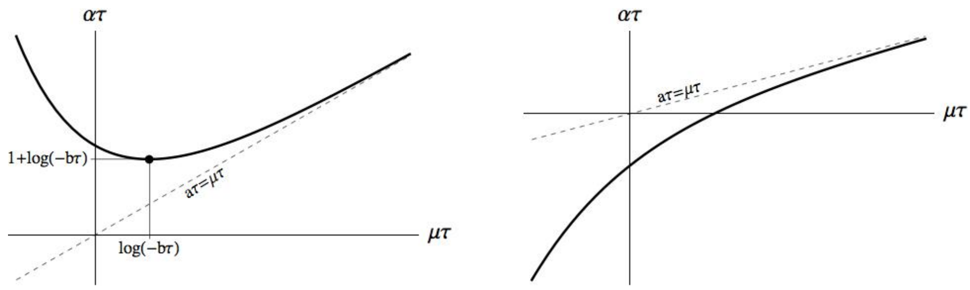


FIGURE 3. Graph of $a\tau$ as a function of $\mu\tau$ for fixed $b\tau > 0$ (left) and $b\tau \leq 0$ (right).

From the left panel it can be seen that if $b\tau < 0$ and $a\tau < 1 + \log(-b\tau)$, equation (15) cannot be satisfied for any $\mu\tau$, while if $a\tau > 1 + \log(-b\tau)$, there are two values of $\mu\tau$ that satisfy the equation, and hence there are two real eigenvalues. From the right panel, however, it can be seen that for every choice of $(a\tau, b\tau)$ there can be found a $\varphi\tau$ that satisfy the equation, and hence there always exists a real eigenvalue.

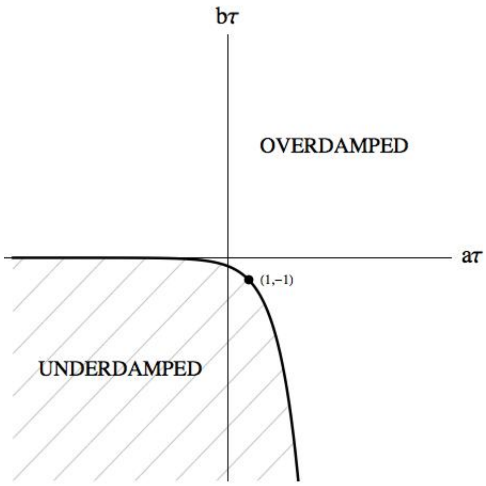


FIGURE 4. The region in the $(a\tau, b\tau)$-plane where $b\tau < 0$ and $a\tau < 1 + \log(-b\tau)$.

3.3. **Example – continued.** Let us now apply the above theory the example developed in section 3.1, i.e.,

$$\frac{dx}{dt} = \beta e^{-\alpha\tau} x_\tau - \delta x - \frac{1}{2}\gamma x^2 \tag{16}$$

The equilibrium is found by equating the right hand side with zero, which gives

$$\bar{x} = \frac{2}{\gamma}\left(\beta e^{-\alpha\tau} - \delta\right) \tag{17}$$

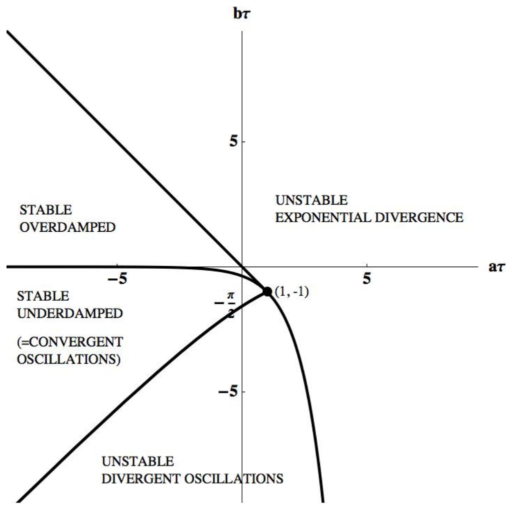


FIGURE 5. Stability boundaries for the system $\frac{du}{dt} = au + bu_\tau$.

The coefficients $a\tau$ and $b\tau$ are

$$a\tau = \delta\tau - 2\beta\tau e^{-\alpha\tau} \quad \text{and} \quad b\tau = \beta\tau e^{-\alpha\tau} \tag{18}$$

From this we immediately see that the $\bar{x} > 0$ if and only if $a\tau + b\tau < 0$ (white region in the next figure). Moreover, we have

$$b\tau = \frac{1}{2}(\delta\tau - a\tau) \tag{19}$$

whenever $\bar{x} > 0$. Thus, $(a\tau, b\tau)$ is constraint to a half-line that lies entirely in the "stable and overdamped"-region (see figure).

Hence we conclude that in the example with a fixed delay the positive equilibrium, whenever it exists, is stable and over-damped.

3.4. **Distributed delays.** Consider the general DDE for a single distributed delay

$$\frac{dx}{dt} = f(x, x_\phi) \tag{20}$$

where

$$x_\phi(t) = \int_0^\infty x(t-\tau)\phi(\tau)d\tau \tag{21}$$

for some probability density ϕ. Suppose $\bar{x}$ is an equilibrium, i.e., $f(\bar{x}, \bar{x}) = 0$. To study the stability properties of $\bar{x}$, let $u = x - \bar{x}$ and $u_\phi = x_\phi - \bar{x}$ denote perturbations from the equilibrium. Then, as a linear approximation of the DDE

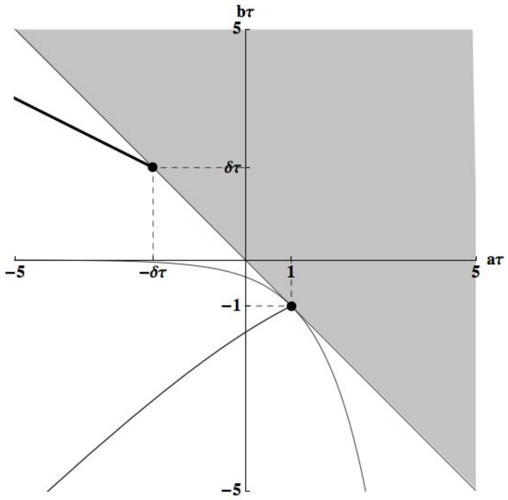


FIGURE 6. Stability in the delayed logistic $\frac{dx}{dt} = \beta x_\tau e^{-\int_0^\tau \alpha(s)ds} - \delta x - \frac{1}{2}\gamma x^2$. For points $(a\tau, b\tau)$ inside the grey region no positive equilibrium exists.

for small perturbations, we have

$$\frac{du}{dt} = au + bu_\phi \tag{22}$$

where

$$a = \partial_x f(\bar{x}, \bar{x}) \quad \text{and} \quad b = \partial_{x_\phi} f(\bar{x}, \bar{x}) \tag{23}$$

Substitution of $u(t) = e^{\lambda t}$ with $\lambda = \mu + i\omega$ gives the characteristic equation

$$\lambda = a + b \int_0^\infty \phi(\tau) e^{-\lambda\tau} d\tau \tag{24}$$

The feasibility of getting any information out of this equation very much depends on the particular choice of ϕ. We shall treat the case of distributed delays by means of example only.

3.4. **Example distributed delay.** Let X denote an adult individual and Y an egg, and consider the following kinds of individual behavior:

$$\begin{array}{rcll} \mathrm{X} & \xrightarrow{\alpha} & \mathrm{X} + \mathrm{Y} & \text{(reproduction)} \\ \mathrm{Y} & \xrightarrow{\beta} & \dagger & \text{(death of an egg)} \\ \mathrm{X} + \mathrm{Y} & \xrightarrow{\gamma} & \mathrm{X} + \dagger & \text{(cannibalism)} \\ \mathrm{X} & \xrightarrow{\delta} & \dagger & \text{(death of an adult)} \\ \mathrm{Y} & \stackrel{\varphi}{\Longrightarrow} & \mathrm{X} & \text{(hatching)} \end{array} \tag{25}$$

The rate at population level with which eggs were being produced at time $t-\tau$ is

$$\alpha x(t-\tau) \tag{26}$$

The survival probability that an egg that was produced at time $t-\tau$ is still alive at time t is equal to

$$e^{-\beta\tau-\gamma\int_{t-\tau}^{t}x(s)ds} \tag{27}$$

The probability density that an egg that was produced at time $t-\tau$ will hatch at time t, given that it is still alive at time t, is equal to $\varphi(\tau)$. Putting all this together we find that the rate of recruitment of new adults into the population is

$$\int_0^\infty \varphi(\tau)\alpha x(t-\tau)e^{-\beta\tau-\gamma\int_{t-\tau}^{t}x(s)ds}d\tau \tag{28}$$

Taking adult deaths into account, we finally get as population equation

$$\frac{dx(t)}{dt} = \int_0^\infty \varphi(\tau)\alpha x(t-\tau)e^{-\beta\tau-\gamma\int_{t-\tau}^{t}x(s)ds}d\tau - \delta x(t) \tag{29}$$

Suppose all probability mass of φ is concentrated at a specific value of τ (i.e., φ is Dirac-delta distribution). Then

$$\frac{dx(t)}{dt} = \alpha x(t-\tau)e^{-\beta\tau-\gamma\int_{t-\tau}^{t}x(s)ds} - \delta x(t) \tag{30}$$

Let ψ be the *uniform distribution* on the interval $(0,\tau)$. Then we can write the above more elegantly as

$$\frac{dx}{dt} = \alpha x_\tau e^{-\beta\tau-\gamma\tau x_\psi} - \delta x \tag{31}$$

where $x_{\tau_0} = x(t-\tau_0)$ and

$$x_\psi(t) = \int_0^\infty \psi(\tau)x(t-\tau)d\tau \tag{32}$$

Now, this is interesting: although we assume a fixed time till hatching, we still have a distributed delay in the exponent. Moreover, we also have a fixed delay in front of the exponential.

Equation (31) has a positive equilibrium

$$\bar{x} = \frac{\log(\alpha/\delta)-\beta\tau}{\gamma\tau} > 0 \tag{33}$$

whenever $\log(\alpha/\delta)-\beta\tau > 0$. To determine the stability of $\bar{x}$, define $u = x-\bar{x}$, $u_\tau = x_\tau - \bar{x}$ and $u_\psi = x_\psi - \bar{x}$. Then, as linear approximation of equation (31), we get

$$\frac{du}{dt} = -\delta u + \delta u_\tau - \delta\Big(\log\frac{\alpha}{\delta} - \beta\tau\Big)u_\psi \tag{34}$$

Substitution of $u(t) = e^{\lambda t}$ with $\lambda = \mu + i\omega$ gives the characteristic equation

$$\lambda\tau = \Big(a\tau\lambda\tau + b\tau\Big)\frac{1 - e^{-\lambda\tau}}{\lambda\tau} \tag{35}$$

where

$$a\tau = -\delta\tau \quad \text{and} \quad b\tau = -\delta\tau\big(\log(\alpha/\delta) - \beta\tau\big) \tag{36}$$

Obviously, $a\tau < 0$. But also $b\tau < 0$ whenever $\bar{x} > 0$.

To find the zero-crossings of the real parts of *complex eigenvalues*, let $\lambda = i\omega \neq 0$. Splitting the real and imaginary parts of the characteristic equation gives

$$\begin{cases} 0 &= a\tau\big(1 - \cos(\omega\tau)\big) + b\tau\frac{\sin(\omega\tau)}{\omega\tau} \\ b\tau &= a\tau\sin(\omega\tau) - b\tau\frac{1-\cos(\omega\tau)}{\omega\tau} \end{cases} \tag{37}$$

Solving for $a\tau$ and $b\tau$ gives

$$\begin{cases} a\tau &= \frac{1}{2}\omega\tau\cot\left(\frac{\omega\tau}{2}\right) \\ b\tau &= -\frac{(\omega\tau)^2}{2} \end{cases} \tag{38}$$

which describes a parameterized curve in the $(a\tau, b\tau)$-plane (solid line in next figure).

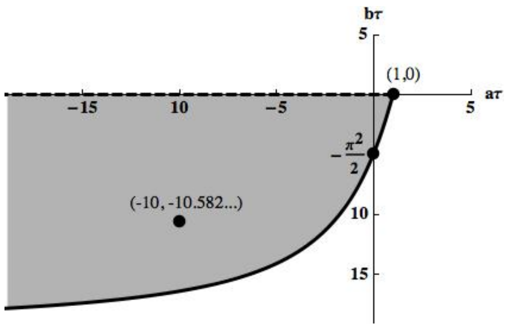


FIGURE 7. Stability (grey) and instability (white). Only the negative quadrant can be interpreted in the cannibalism model.

To find the zero-crossings of *real eigenvalues* we set $\lambda = 0$. This gives simply $b\tau = 0$ (dashed line in the above figure). To find which region corresponds to stability and which to instability, we use a calibration point: substitute, e.g., $\lambda = -1$ and $a\tau = -10$ into the characteristic equation (35) and solve for $b\tau$. This gives $b\tau = -10.582\ldots$. Putting it the other way: the point $(a\tau, b\tau) = (-10, -10.582\ldots)$ gives $\lambda = -1$ and hence lies inside the stability region (see above figure).

The expressions in (36) show that only $a\tau < 0$ and $b\tau < 0$ are possible. Varying the model parameters $\alpha, \ldots, \delta$ and/or the fixed delay time τ affects the $a\tau$ and the

$b\tau$ (and hence the stability of the equilibrium) according to equations (36). An example of how is shown in the following figure.

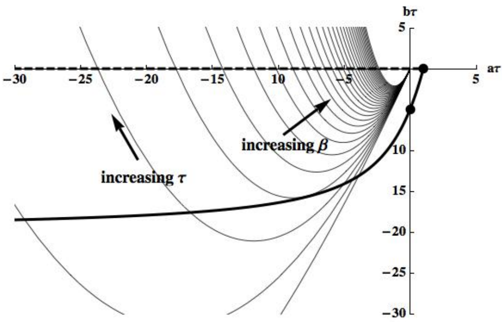


FIGURE 8. The effect of the delay τ and the density-independent egg mortality β on $(a\tau, b\tau)$. Changes in τ cause a movement along the (thin) curves, while changes in β cause a movement across the curves as indicated.

It can be seen that increasing the delay time τ initially leads to a loss of stability, but eventually stability is regained. Increasing egg mortality β has a stabilizing effect, but the positive equilibrium becomes smaller and reaches zero once $b\tau = 0$.