# Homework 3

Due Friday, July 14 2017

## Problem 1 (10 points)

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The Beverton-Holt difference equation is given by

$$N_{t+1} = \frac{rKN_t}{K + (r-1)N_t}, \tag{1}$$

is widely used in the model of fisheries. Here, $N_t$ is the population density of fish at time $t$ and $r > 1$ is the "inherent growth rate" of the population and $K > 0$ is the carrying capacity.

(a) Find all the equilibria of this model and determine their stability. (You may want to use graphical approaches to check your results, but you should determine stability analytically.)

(b) Make the substitution $x_t = 1/N_t$ and show that this is a linear, inhomogeneous difference equation. Use this to find an explicit formula for $N_t$ in terms of only $r$, $K$ and $N_0$. Compare this solution to that of the logistic equation from homework 2.

(c) Now let $\mu = (r-1)/r$ and show that equation (1) can be rewritten as

$$N_{t+1} - N_t = \mu N_{t+1} \left(1 - \frac{N_t}{K}\right). \tag{2}$$

Use this to explain why the Beverton-Holt model is an approximation of the logistic equation.

## Part (a)

Equilibria of (1) are values of $N$ where

$$N = f(N) = \frac{rKN}{K + (r-1)N}, \tag{3}$$

so

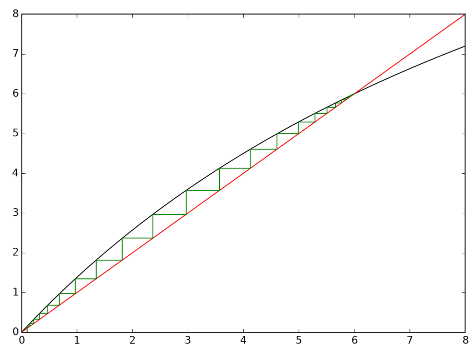
$$\begin{aligned}KN + (r-1)N^2 &= rKN, \text{ and}\\ (1-r)KN + (r-1)^2N^2 &= 0, \text{ so}\\ (r-1)N\left(N-K\right)) &= 0.\end{aligned}$$

This means that there are two equilibria at $N^* = 0$ and $N^* = K$. We can determine the stability of these equilibria analytically by calculating $f'(N^*)$. We have

$$f'(N) = \frac{rK\left(K + (r-1)N\right)\right) - (r-1)rKN}{(K+(r-1)N)^2} = \frac{rK^2}{(K+(r-1)N)^2}. \tag{4}$$

We therefore have $f'(0) = r > 1$, so $N^* = 0$ is always an unstable node. Likewise, $f'(K) = 1/r \in (0,1)$, so $N^* = K$ is always a stable node.

As an example, this is the cobweb diagram when $r = 1.5$ and $K = 6$. Other parameter values look essentially the same.




## Part (b)

If we let $x_t = 1/N_t$, then we have

$$\frac{1}{x_{t+1}} = \frac{rK/x_t}{K + (r-1)/x_t} = \frac{rK}{Kx_t + (r-1)},$$

so

$$x_{t+1} = \frac{1}{r}x_t + \frac{r-1}{rK}.$$

This is a linear, inhomogeneous difference equation. We already solved the problem $x_{t+1} = ax_t + b$ in class, and we found that

$$x_t = \left(x_0 - \frac{b}{1-a}\right)a^t + \frac{b}{1-a}.$$

In our problem, $a = 1/r$ and $b = (r-1)/(rK)$, so we have

$$x_t = \left(x_0 - \frac{r-1}{rK(1-1/r)}\right)\left(\frac{1}{r}\right)^t + \frac{r-1}{rK(1-1/r)} = \left(x_0 - \frac{1}{K}\right) r^{-t} + \frac{1}{K}.$$

Substituting $x_t = 1/N_t$, we find that

$$\frac{1}{N_t} = \frac{1 + (K/N_0 - 1)r^{-t}}{K},$$

so

$$N_t = \frac{KN_0}{N_0 + (K - N_0)r^{-t}} = \frac{KN_0 r^t}{K - N_0 + N_0 r^t}. \tag{5}$$

The solution to the logistic differential equation from homework 2 is

$$N(t) = \frac{KN_0 e^{rt}}{K - N_0 + N_0 e^{rt}}. \tag{6}$$

These two are nearly identical – the only difference is that we have geometric growth terms ($r^t$) for the Beverton-Holt equation and exponential growth terms ($e^{rt}$) for the logistic equation.

## Part (c)

Equation (1) can be rewritten as

$$N_{t+1}\left(K + (r-1)N_t\right) = rKN_t,$$

so

$$\begin{aligned} 0 &= N_t - \frac{1}{r}N_{t+1}\left(1 + (r-1)\frac{N_t}{K}\right), \text{ so} \\ 0 &= N_t - \frac{r-1}{r}N_{t+1}\left(\frac{1}{r-1} + \frac{N_t}{K}\right) \text{ and therefore} \\ 0 &= N_t - \frac{r-1}{r}N_{t+1}\left(\frac{r}{r-1} - 1 + \frac{N_t}{K}\right), \text{ so} \\ 0 &= N_t - N_{t+1} - \mu N_{t+1}\left(1 - \frac{N_t}{K}\right). \end{aligned}$$

Therefore,

$$N_{t+1} - N_t = \mu N_{t+1}\left(1 - \frac{N_t}{K}\right), \tag{7}$$

as desired.

Recall that the logistic equation is given by

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \mu N(t)\left(1 - \frac{N(t)}{K}\right). \tag{8}$$

We can approximate

$$\frac{\mathrm{d}N}{\mathrm{d}t} \approx \frac{N(t+\Delta t) - N(t)}{\Delta t},$$

and $N(t) \approx N(t + \Delta t)$. Substituting these into the logistic equation, we get

$$\frac{N(t+\Delta t) - N(t)}{\Delta t} \approx \mu N(t+\Delta t)\left(1 - \frac{N(t)}{K}\right).$$

In particular, if we choose $\Delta t = 1$ and write $N(t) = N_t$, then we have

$$N_{t+1} - N_t \approx \mu N_{t+1}\left(1 - \frac{N_t}{K}\right), \tag{9}$$

which is the same as the Beverton-Holt equation.

## Problem 2 (5 points)

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The Ricker model is another difference equation used widely in fisheries biology. It is given by

$$N_{t+1} = N_t e^{r[1-N_t/K]}, \tag{10}$$

where $N_t$ is the population density of fish at time $t$ and $r$ is the per capita growth rate and $K$ is the carrying capacity. Find the fixed points of this map and determine their stability analytically. Draw a cobweb diagram for this map with a reasonable choice of $r$ and $N_0$.

## Solution

To find the fixed points of (10), we need to set

$$f(N) \equiv Ne^{r[1-N/K]} = N.$$

One solution to this equation is plainly $N^* = 0$. If $N \neq 0$, then we can divide through by $N$, so we have

$$\begin{aligned} e^{r[1-N/K]} &= 1, \text{ so} \\ r\,[1 - N/K] &= 0, \text{ and therefore} \\ 1 - N/K &= 0, \end{aligned}$$

and so $N^* = K$.

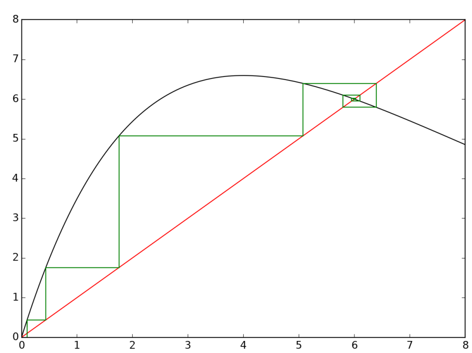
To determine the stability of these equilibria, we need to find $f'(N^*)$. We have

$$f'(N) = e^{r[1-N/K]} - \frac{rN}{K} e^{r[1-N/K]}.$$

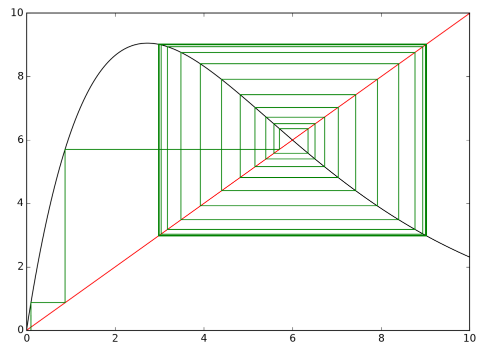
This means that $f'(0) = e^r$. Since $f'(0) > 1$ if $r > 0$ and $0 < f'(0) < 1$ if $r < 0$, we know that $N^* = 0$ is a stable node when $r < 0$ and an unstable node when $r > 0$.

Likewise, $f'(K) = 1 - r$. This means that $f'(K) > 1$ if $r < 0$ and $0 < f'(K) < 1$ if $0 < r < 1$ and $-1 < f'(K) < 0$ if $1 < r < 2$ and $f'(K) < -1$ if $r > 2$. In summary, $N^* = K$ is stable if $0 < r < 2$ and unstable otherwise. It is a node if $r < 1$ and a spiral if $r > 1$.

We can confirm these results graphically. For example, when $r = 1.5$ and $K = 6$, we obtain the following cobweb diagram:




and when $r = 2.2$ and $K = 6$ we obtain:




## Problem 3 (15 points)

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We proposed using the logistic map

$$x_{t+1} = \mu x_t(1 - x_t) \tag{11}$$

as a model of eel population growth. We argued that the growth rate should depend on how crowded the population was at an earlier time, not just on how crowded it is now. By this argument, it would probably be more accurate to use the following model (known as the *lagged logistic map* or *delayed logistic map*):

$$x_{t+1} = \mu x_t(1 - x_{t-\tau}), \tag{12}$$

where $\tau$ is a positive integer. We can think of this model as saying that the population depends on both how large the population is now ($x_t$) and how large the population was $\tau$ years ago ($x_{t-\tau}$). This seems somewhat reasonable – the population right now tells us how many breeding adults there are, which we certainly need to take into account, and the population $\tau$ years ago influences how much competition there was when the current adults were growing. This model is reasonable if, for instance, juvenile nutrition has a substantial effect on breeding success later in life.

(a) Show that equation (12) has two equilibria at $x^* = 0$ and $x^* = 1 - 1/\mu$. Note that $x^*$ is an equilibrium if $x_{t+1} = x_t = x_{t-\tau} = x^*$.

(b) To determine the stability of equilibria for a delay difference equation $x_{t+1} = f(x_t, x_{t-\tau})$, we first need to find the linearization of our map. For delay equations, this linearization is given by

$$x_{t+1} \approx \left.\frac{\partial f(x,y)}{\partial x}\right|_{x=y=x^*} x_t + \left.\frac{\partial f(x,y)}{\partial y}\right|_{x=y=x^*} x_{t-\tau}. \tag{13}$$

Show that the linearization about $x^* = 0$ is given by

$$x_{t+1} \approx \mu x_t, \tag{14}$$

and that the linearization about $x^* = 1 - 1/\mu$ is given by

$$x_{t+1} \approx x_t + (1-\mu)x_{t-\tau}. \tag{15}$$

(c) In order to solve the linearized equations you found in part (b), we will try solutions of the form $x_t = \lambda^t$. Show that there is only one such solution to (14) and find the value of $\lambda$. Show that there are $\tau + 1$ possible solutions (i.e., $\tau + 1$ values of $\lambda$) to (15) and that these solutions satisfy

$$\mu = \lambda^\tau (1-\lambda) + 1. \tag{16}$$

(d) Show that if $\mu < 1$, there is only one positive real solution $\lambda$ of equation (16), and that this $\lambda$ is larger than 1. In addition, show that there are two positive real solutions to (16) if $\mu$ is slightly larger than 1, and that both solutions are smaller than 1. Finally, show that if $\mu$ is too large, then there are no positive real solutions to (16). You may use graphical arguments for this part – you do not need to calculate the values of $\lambda$ analytically.

(e) We are interested in the onset of oscillatory behavior. The equilibrium $x^* = 1 - 1/\mu$ will become a spiral instead of a node when the positive, real solutions of (16) disappear. The critical value $\mu_o$ where this occurs is the maximum value of (15). Calculate $\mu_o$ by setting $\mathrm{d}\mu/\mathrm{d}\lambda = 0$. Show that $\mu_o$ is a decreasing function of $\tau$ and that

$$\lim_{\tau\to\infty} \mu_o(\tau) = 1. \tag{17}$$

This means that larger delays make it easier to produce oscillations.

## Part (a)

Throughout this problem, we will define

$$f(x,y) = \mu x\,(1-y)\,. \tag{18}$$

Equation (12) has an equilibrium at $x^*$ if and only if

$$f(x^*, x^*) \equiv \mu x^* (1 - x^*) = x^*.$$

If $x^* = 0$, then we have

$$f(0, 0) = \mu \cdot 0 \cdot (1 - 0) = 0,$$

so $x^* = 0$ is an equilibrium. Likewise, if $x^* = 1 - 1/\mu$ then

$$f\left(1 - \frac{1}{\mu}, 1 - \frac{1}{\mu}\right) = \mu\left(1 - \frac{1}{\mu}\right)\left(1 - 1 + \frac{1}{\mu}\right) = 1 - \frac{1}{\mu},$$

so $x^* = 1 - 1/\mu$ is also an equilibrium.

## Part (b)

We have

$$\frac{\partial f(x,y)}{\partial x} = \mu(1 - y) \quad \text{and} \quad \frac{\partial f(x,y)}{\partial y} = -\mu x.$$

This means that the linearization about $x^* = 0$ is given by

$$\begin{aligned} x_{t+1} &\approx \left.\frac{\partial f(x,y)}{\partial x}\right|_{x=y=0} x_t + \left.\frac{\partial f(x,y)}{\partial y}\right|_{x=y=0} x_{t-\tau} \\ &= \mu(1 - 0)\, x_t - \mu \cdot 0 x_{t-\tau} \\ &= \mu x_t. \end{aligned}$$

Similarly, the linearization about $x^* = 1 - 1/\mu$ is given by

$$\begin{aligned} x_{t+1} &\approx \left.\frac{\partial f(x,y)}{\partial x}\right|_{x=y=1-1/\mu} x_t + \left.\frac{\partial f(x,y)}{\partial y}\right|_{x=y=1-1/\mu} x_{t-\tau} \\ &= \mu\left(1 - 1 + \frac{1}{\mu}\right) x_t + -\mu\left(1 - \frac{1}{\mu}\right) x_{t-\tau} \\ &= x_t + (1 - \mu)\, x_{t-\tau}. \end{aligned}$$

## Part (c)

If we substitute a solution of the form $x_t = \lambda^t$ into (14), then we get

$$x_{t+1} = \lambda^{t+1} = \mu \lambda^t.$$

Dividing both sides by $\lambda$, we find that $\lambda = \mu$, so the only non-trivial solution to this problem is $x_t = \mu^t$.

Similarly, if we substitute this into equation (15), we obtain

$$\lambda^{t+1} = \lambda^t + (1-\mu)\lambda^{t-\tau}.$$

If we divide both sides by $\lambda^{t-\tau}$, we find that

$$\lambda^{\tau+1} = \lambda^\tau + (1-\mu),$$

so

$$\mu = \lambda^\tau (1-\lambda) + 1,$$

as desired. This is a $\tau+1$st degree polynomial in $\lambda$, so it has $\tau+1$ solutions (although some of them may be complex).

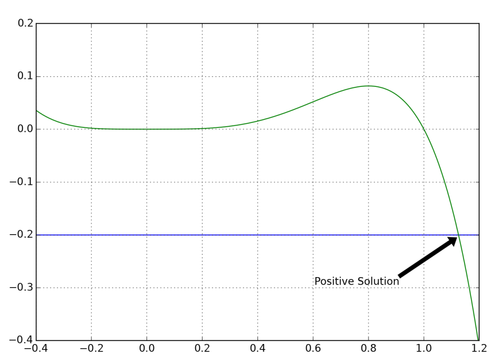
## Part (d)

For $\tau > 2$, we cannot hope to solve this equation explicitly, but it is relatively easy to find the solutions graphically. To do so, note that

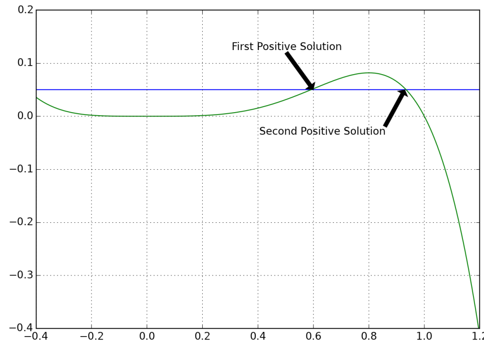
$$\mu - 1 = \lambda^\tau(1-\lambda).$$

To solve this equation, we can plot $y_1 = \mu - 1$ and $y_2 = \lambda^\tau(1-\lambda)$ in the same figure and find where they intersect. The first graph is simple, since $y_1$ is constant. The second is a high degree polynomial, but it is already factored and so straightforward to plot. We know that $y_2$ has a $\tau$th order root at $\lambda = 0$ and a simple root at $\lambda = 1$. We will use $\tau = 4$ as an example, but the behavior is similar for any $\tau$. (Graphs with odd values of $\tau$ will look very different for $\lambda < 0$, but we are only interested in positive real solutions.)

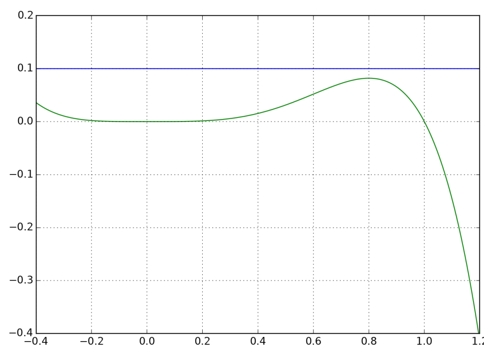
For $\mu < 1$, we have that $\mu - 1 < 0$, so our graph looks like:



Notice that the only intersection point is at $\lambda > 1$. With $\mu$ slightly larger than 1, our graph instead looks like:




Here there are two positive intersections, and they are both between 0 and 1, so we have positive real solutions $0 < \lambda_1 < \lambda_2 < 1$. If we choose $\mu$ too large, then our graph instead looks like:




In this case there are no positive intersections, which means that there are no positive real solutions of (16).

## Part (e)

As should be clear from the graphs in the previous section, positive real solutions to (16) cease to exist when $\mu$ is larger than the maximum value of $\mu(\lambda)$ for $\lambda > 0$. We can find this by setting $\mathrm{d}\mu/\,\mathrm{d}\lambda = 0$. This means that

$$\begin{aligned}\frac{\mathrm{d}\mu}{\mathrm{d}\lambda} &= \tau\lambda^{\tau-1}(1-\lambda) - \lambda^{\tau}\\ &= \tau\lambda^{\tau-1} - \tau\lambda^{\tau} - \lambda^{\tau}\\ &= \lambda^{\tau-1}(\tau - (\tau+1)\lambda)\\ &= 0.\end{aligned}$$

This has two solutions: $\lambda = 0$, which corresponds to a minimum of $\mu$, and

$$\lambda_{max} = \frac{\tau}{\tau+1}.$$

We therefore have

$$\begin{aligned}\mu_0(\tau) = \mu(\lambda_{\max}) &= \left(\frac{\tau}{\tau+1}\right)^{\tau}\left(1 - \frac{\tau}{\tau+1}\right) + 1\\ &= \left(\frac{\tau}{\tau+1}\right)^{\tau}\left(\frac{1}{\tau+1}\right) + 1\end{aligned}$$

Notice that

$$\frac{\mathrm{d}\mu_0}{\mathrm{d}\tau} = \frac{1}{\tau+1}\left(\frac{\tau}{\tau+1}\right)^{\tau}\ln\left(\frac{\tau}{\tau+1}\right),$$

which is strictly negative for all $\tau > 1$, so $\mu_0$ is a decreasing function of $\tau$. To find the limit as $\tau$ goes to infinity, notice that

$$\left(\frac{\tau}{\tau+1}\right)^{\tau} = \left(1 + \frac{1}{\tau}\right)^{-\tau}.$$

We therefore have

$$\lim_{\tau\to\infty}\left(\frac{\tau}{\tau+1}\right)^{\tau} = \lim_{\tau\to\infty}\left(1+\frac{1}{\tau}\right)^{-\tau} = e^{-1},$$

which we proved in the first week of class. Therefore,

$$\begin{aligned}\lim_{\tau\to\infty}\mu_0(\tau) &= \lim_{\tau\to\infty}\left[\left(\frac{\tau}{\tau+1}\right)^{\tau}\frac{1}{\tau+1} + 1\right]\\ &= \lim_{\tau\to\infty}\left[\left(\frac{\tau}{\tau+1}\right)^{\tau}\right]\cdot\lim_{\tau\to\infty}\left[\frac{1}{\tau+1}\right] + 1\\ &= e^{-1}\cdot 0 + 1\\ &= 1.\end{aligned}$$

## Problem 4 (10 points)

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Another way to introduce a delay to the logistic equation is to assume that the density at all times in the past influences the per capita growth rate, and to assign a weight $\kappa$ to each past density. For instance, we can write

$$\frac{\mathrm{d}x}{\mathrm{d}t} = rx(t)\int_0^\infty \kappa(\tau)\left(1 - x(t-\tau)\right)\,\mathrm{d}\tau, \tag{19}$$

with

$$\kappa(\tau) = \alpha e^{-\alpha\tau}, \tag{20}$$

for some constant $\alpha > 0$. To solve this equation, we need to give an initial condition $x$ for all past times. That is, we need to specify some function $x_0(t)$ such that

$$x(t) = x_0(t) \text{ for all } t \le 0. \tag{21}$$

Equation (19) is called a Volterra integrodefferential equation.

(a) Show that $x(t) = 0$ for all $-\infty < t < \infty$ is a solution to (19). Show that $x(t) = 1$ for all $-\infty < t < \infty$ is a solution to (19). This means that 0 and 1 are equilibria of this equation.

(b) The linearization of (19) about $x^* = 1$ is

$$\frac{\mathrm{d}x}{\mathrm{d}t} \approx -r\int_0^\infty \kappa(\tau)x(t-\tau)\,\mathrm{d}\tau. \tag{22}$$

Solve equation (22) by trying a solution of the form $x(t) = e^{\lambda t}$. (You do not need to worry about initial conditions.)

(c) The equilibrium $x^* = 1$ is called stable if every $\lambda$ you found in part (b) has negative real part. Find conditions on $\alpha$ and $r$ such that $x^* = 1$ is stable.

## Part (a)

If $x(t) = 0$ for all time, then $x(t-\tau)$ is also zero for all $t$ and $\tau$, and $x'(t) = 0$ for all $t$. Substituting these into (19), we obtain

$$0 = \frac{\mathrm{d}x}{\mathrm{d}t} = rx(t)\int_0^\infty \kappa(\tau)x(t-\tau)\,\mathrm{d}\tau = r\cdot 0\cdot\int_0^\infty \kappa(\tau)\left(1-0\right)\,\mathrm{d}\tau = 0.$$

This means that $x(t) = 0$ is a solution of (19), so $x^* = 0$ is an equilibrium of the equation.

Likewise, if $x(t) = 1$ for all time, then $x(t-\tau)$ is also one for all $t$ and $\tau$ and $x'(t) = 0$ for all $t$. Substituting these into (19), we obtain

$$0 = \frac{\mathrm{d}x}{\mathrm{d}t} = rx(t)\int_0^\infty \kappa(\tau)x(t-\tau)\,\mathrm{d}\tau = r\cdot 1\cdot\int_0^\infty \kappa(\tau)\cdot 0\,\mathrm{d}\tau = 0.$$

This means that $x(t) = 1$ is also a solution of (19), and therefore $x^* = 1$ is an equilibrium.

## Part (b)

If $x(t) = e^{\lambda t}$, then $x(t-\tau) = e^{\lambda(t-\tau)}$ and $x'(t) = \lambda e^{\lambda t}$. Substituting these into (22), we have

$$\begin{aligned}
\lambda e^{\lambda t} &= -r\int_0^\infty \kappa(\tau)e^{\lambda(t-\tau)}\,\mathrm{d}\tau \\
&= -r\int_0^\infty \alpha e^{-\alpha\tau}e^{\lambda(t-\tau)}\,\mathrm{d}\tau \\
&= -r\alpha e^{\lambda t}\int_0^\infty e^{-(\alpha+\lambda)\tau}\,\mathrm{d}\tau \\
&= -r\alpha e^{\lambda t}\left[-\frac{1}{\alpha+\lambda}e^{-(\alpha+\lambda)\tau}\right]_{\tau=0}^{\tau=\infty} \\
&= \frac{-r\alpha}{\alpha+\lambda}e^{\lambda t}.
\end{aligned}$$

We therefore have

$$\begin{aligned}
\lambda &= \frac{-r\alpha}{\alpha+\lambda}, \text{ so} \\
\lambda^2 + \alpha\lambda + r\alpha &= 0.
\end{aligned}$$

This is a quadratic in $\lambda$, so we have

$$\lambda_1 = \frac{-\alpha + \sqrt{\alpha^2 - 4r\alpha}}{2} \quad\text{and}\quad \lambda_2 = \frac{-\alpha - \sqrt{\alpha^2 - 4r\alpha}}{2}.$$

Since we have two values of $\lambda$, we have obtained two solutions to (22). In particular, $x_1(t) = e^{\lambda_1 t}$ and $x_2(t) = e^{\lambda_2 t}$ are both solutions.

## Part (c)

The equilibrium $x^* = 1$ is stable if the real parts of $\lambda_1$ and $\lambda_2$ are both negative. Notice that if the $\lambda$'s are complex, then their real parts are both $-\alpha/2$. Since we assumed $\alpha > 0$, this means that $x^* = 1$ is stable whenever the $\lambda$'s aren't real. If $\lambda_1$ and $\lambda_2$ are real, then $\lambda_2$ is certainly negative (since $\alpha > 0$), so we really only need to check $\lambda_1$. That is, we need

$$\begin{aligned} -\alpha + \sqrt{\alpha^2 - 4r\alpha} &> 0, \text{ so} \\ \sqrt{\alpha^2 - 4r\alpha} &< \alpha, \text{ which means} \\ \alpha^2 - 4r\alpha &< \alpha^2, \text{ so} \\ r\alpha &> 0. \end{aligned}$$

(Note that we need to be careful when squaring both sides of an inequality, since we might be multiplying by a negative value and therefore need to flip our inequality. In this case, both sides of the inequality were positive so there was no issue.) We can only have $r\alpha > 0$ if both $r$ and $\alpha$ have the same sign. Since $\alpha > 0$, this means that $x^* = 1$ is stable if and only if both $\alpha > 0$ and $r > 0$.