Biol 301 (Spring 2001): Solutions to Problem Set #4:

1. (a) In figure 1, at $x = 0$, the value of $f(x) = \lambda/(1 + x)^b$ is $f(0) = \lambda$, namely $\lambda = 1$ and $\lambda = 2$. For a given λ, b causes the curve to decrease more quickly initially (b ranges from 1 to 3 in the figure).

   (b) In figure 2, the upper two curves are for $\lambda = 1, 2$ and $b = 1$. The middle two curves are for $\lambda = 1, 2$ and $b = 2$. The lower two curves are for $\lambda = 1, 2$ and $b = 3$. For $b = 1$, the function $x(t + 1)$ has an asymptotic value at $y = \lambda$. For larger b the function $x(t + 1)$ asymptotes at $y = 0$. For a given λ, increasing b causes the function to take on a lower maximum and descend more rapidly to the right of the maximum. For a given b, an increase in λ causes the function to have a higher maximum value and descend more rapidly to the right of the maximum.

   (c) The carrying capacity is given by the solution of $x^* = \frac{\lambda x^*}{(1+x^*)^b} x^* = \frac{\lambda x^*}{(1+x^*)^b}$. Cancelling x^* on the left and in the numerator on the right yields $1 = \frac{\lambda}{(1+x^*)^b}$, cross multiplication yields $(1 + x^*)^b = \lambda$, rising each side to the power $1/b$ yields,$(1 + x^*) = \lambda^{1/b}$, subtracting 1 from each side yields the equilibrium, $x^* = \lambda^{1/b} - 1$. Note that the value $x = 0$ also satisfies conditions of an equilibrium.

   (d) To determine the stability conditions of the equilibrium $x^* = \lambda^{1/b}-1$, we employ stability analysis. Stability analyses consists of taking the derivative of the function $F(x(t)) = x(t + 1)$ and then evaluating the derivative at the equilibrium point x^*. For $F(x) = \frac{\lambda x}{(1+x)^b}$ we have

$$\frac{dF}{dx} = \frac{(1 + x)^b\lambda - b(1 + x)^{b-1}\lambda x}{(1 + x)^{2b}} = \frac{\lambda}{(1 + x)^b} - \frac{\lambda b x}{(1 + x)^{b+1}}$$

   Evaluating $\frac{dF}{dx}$ at $x^* = \lambda^{1/b} - 1$ yields:

$$\begin{aligned}
\frac{dF}{dx}(\lambda^{1/b} - 1) &= \frac{\lambda}{(1 + \lambda^{1/b} - 1)^b} - \frac{\lambda b(\lambda^{1/b} - 1)}{(1 + \lambda^{1/b} - 1)^{b+1}} \\
&= \frac{\lambda}{\lambda} - \frac{\lambda b(\lambda^{1/b} - 1)}{\lambda^{(b+1)/b}} \\
&= 1 - \frac{\lambda^{(b+1)/b} b}{\lambda^{(b+1)/b}} + \frac{\lambda b}{\lambda^{(b+1)/b}} \\
&= 1 - b + b\lambda^{-1/b} \\
&= 1 - b(1 - \frac{1}{\lambda^{1/b}})
\end{aligned}$$

   For the equilibrium to be stable the absolute value of $\frac{dF}{dx}(\lambda^{1/b} - 1)$ must be less than 1. Note that the derivative of $F(x)$ at the equilibrium is always < 1 (why?), so that the critical condition for stability is $\frac{dF}{dx}(\lambda^{1/b} - 1) > -1$. In other word, the slope of F at the equilibrium should not be too negative. In Mathematica you could plot $\frac{dF}{dx}(\lambda^{1/b}-1) = 1-b(1-\frac{1}{\lambda^{1/b}})$ to get an idea of the values of b and λ that yield values of $\frac{dF}{dx}(\lambda^{1/b}-1)$ bigger than -1. A more precise way is to to consider the inequality $\frac{dF}{dx}(\lambda^{1/b} - 1) = 1 - b(1 - \frac{1}{\lambda^{1/b}}) > -1$, which yields $-1 < 1 - b(1 - \frac{1}{\lambda^{1/b}})$, hence $-2 < -b(1 - \frac{1}{\lambda^{1/b}})$. Thus we see that if $-b(1 - \frac{1}{\lambda^{1/b}}) > -2$, then the equilibrium is stable.

(e) Example for cobwebbing: in Figure 3, $g = x(t + 1)$ versus $x(t)$ is plotted in which $\lambda = 2$ and $b = 2$. Our analysis predicts that the carrying capacity in this case should be $x^* = 2^{1/2} - 1 = 0.414$, which appears to hold true in the figure. The cobwebbing suggests that x^* is stable. Based on our analysis, if this is true then $-b(1-\frac{1}{\lambda^{1/b}}) \geq -2$;a quick check yields $-2(1 - 1/1.414) \geq -2$ or $-1.414 \geq -2$, so this checks out.

2. (a) In figure 4, we see that for $\lambda = 2$, there is a monotonic approach to equilibrium.

   (b) In figure 5, we see that for $\lambda = 5$, the population reaches an equilibrium via dampened oscillations

   (c) In figure 6, for $\lambda = 10$, the population enters a two cycle.

   (d) In figure 7, for $\lambda = 20$, the population enters a four cycle.

   (e) In figure 8, for $\lambda = 40$, the population has chaotic dynamics of population size.

   NOTE: Corroborate these results with observations made in problem 1a,b,d.

3.

$$\begin{aligned}
\ln \frac{x(t)}{x_s(t)} &= \ln \frac{x(t)}{\frac{x(t)}{(1+x(t))^b}} \\
&= \ln(1 + x(t))^b \\
&= b \ln(1 + x(t))
\end{aligned}$$

For large $x(t)$ we have $1 + x(t) \approx x(t)$, and therefore $\ln \frac{x(t)}{x_s(t)} = b\ln(x(t))$ for large $x(t)$, so that

$$\ln \frac{x(t)}{x_s(t)} = b \ln x(t).$$

Now if we let $z = \ln(x(t))$ and $f = \ln \frac{x(t)}{x_s(t)}$, then $f(z) = bz$ which is a linear function with slope b. To measure b in the field, take a sample of initial population sizes $x(t)$, i.e. is the number of individuals at the start of a given year. Then measure the corresponding number of individuals that survive to reproduction, $x_s(t)$, and regress the values of $\ln \frac{x(t)}{x_s(t)}$ on $\ln(x(t))$. The slope of this regression line will give an estimate of b.

4. (a) To solve this problem we have to use the stability analysis of problem 1. In figure 9, we have plotted the curve in the λ, b - plane defined by $-2 = -b(1 - \frac{1}{\lambda^{1/b}})$. All parameter combinations (λ, b) that lie below this curve correspond to populations with stable equilibria, all parameter combinations (λ, b) that lie above this curve correspond to populations with unstable equilibria. Plotting the various combinations given in the table yields the result that the only species that has demographic parameters leading to an unstable equilibrium is the one corresponding to the point (75.0,3.4), i.e the Potato Beetle. As a check:

   $-2 < -0.1(1 - \frac{1}{1.3^{1/0.1}}) = -0.09$ (stable)
   $-2 < -2.1(1 - \frac{1}{2.2^{1/2.1}}) = -0.65$ (stable)
   $-2 < -1.9(1 - \frac{1}{10.6^{1/1.9}}) = -1.35$ (stable)
   $-2 > -3.4(1 - \frac{1}{75^{1/3.4}}) = -2.44$ (unstable)
   $-2 < -0.9(1 - \frac{1}{54^{1/0.9}}) = -0.88$ (stable)

5. (a) In figure 10, the upper two curves are for $\lambda = 2$ and $q = 1$ and $q = 2$. The lower two curves are for $\lambda = 1$ and $q = 1$ and $q = 2$. Note that increasing q causes the curve to descend more rapidly.

   (b) In figure 11, the upper curve and the middle curve that is broader correspond to $\lambda = 2, 1$, respectively and $q = 1$. The second set of curves correspond to $\lambda = 1, 2$ and $q = 2$. We see that as lambda increases the maximum of $x(t+1)$ increases and the curve has a steeper slope to the right of the maximum; as q increases for a given λ, the maximum of $x(t+1)$ is less and q doesn't appear to effect the relative slope of the curve. For practice, determine the value of $x(t)$ where the function $x(t+1)$ has a maximum (ANSWER: $\frac{1}{q}$).

   (c) The carrying capacity is the solution of the equation $x^* = \lambda x^* e^{-qx^*}$. Solving for x^* yields the nonzero solution $x = \frac{\ln \lambda}{q}$.

   (d) As with problem 1, to determine the stability conditions at the carrying capacity, we need to take the derivative of $F(x(x(t))$ and evaluate it at the equilibrium carrying capacity. The condition for stability is that the absolute value of the slope of F at x^* is less than 1.

$$\begin{aligned}\frac{dF}{dx} &= \frac{d}{dx}\lambda x e^{-qx}\\ &= \lambda e^{-qx} - \lambda x q e^{-qx}\end{aligned}$$

   Therefore, $\frac{dF}{dx}(x^*) = \frac{dF}{dx}(\frac{\ln \lambda}{q}) = 1 - \ln \lambda$ upon simplification. For the carrying capacity to be stable we need $1 - \ln \lambda > -1$ (Note that $1 - \ln \lambda$

is always < 1!). Therefore, the stability condition is $\ln \lambda \leq 2$. i.e. the range of stability is $0 < \ln \lambda < 2$. NOTE: The stability conditions are independent of q, which was suggested in the description of figure 11 (the relative slope of the curve for a given λ wasn't effected by q).

(e) In figure 12, $\lambda = 2$ and $q = 1$. Note that for this combination of parameter values the equilibrium is less than the $x(t)$ in which $x(t+1)$ takes on a maximum value.

6. (a) We can use information from #5 to get an idea where to start. Stability analysis suggests for $\ln \lambda > 2$, the population does not have a stable equilibrium and instead exhibits more complicated dynamics. By plotting the trajectory of $x(t+1)$ versus t, indeed you should have found that at about $e^2 = 7.389$ the population exits a stable equilibrium and starts to move on a two cycle. Thus, for $1 < \lambda < 7.389$ the population exhibits a stable equilibrium.

   (b) $7.38 < \lambda < 12.30$

   (c) $12.30 < \lambda < 14.20$

   (d) $14.20 < \lambda < 15.10$

7. In the plot of $x(t + 1)$ versus $x(t)$, small differences between values on the $x(t)$ axis correspond to small differences at time $t + 1$. In stark contrast, in the plot of $x(t + 10)$ versus $x(t)$, small differences in $x(t)$ can correspond to large differences at time $t + 10$. This means that if you initially make a small error in the measurement of the population size at time t, in a chaotic system, this may result in the predicted value being much different from the observed value at time $t + 10$. (see Hastings, Fig. 4.11, p. 98).

8. (a) There are three equilibria: at $x = 0$, at $x \approx 1.1$, and at $x \approx 3.3$.

   (b) Cobwebbing shows that $x \approx 0$ and $x \approx 3.3$ are stable, while the intermediate equilibrium is unstable.

   (c) If the population is perturbed to values below the unstable equilibrium it will go to extinction. This is an example of a population that needs to achieve a threshold population size in order to be viable. This threshold population size is given by the unstable equilibrium: if the population is perturbed to values above this unstable equilibrium, then it will approach the carrying capacity and survive in the long run.

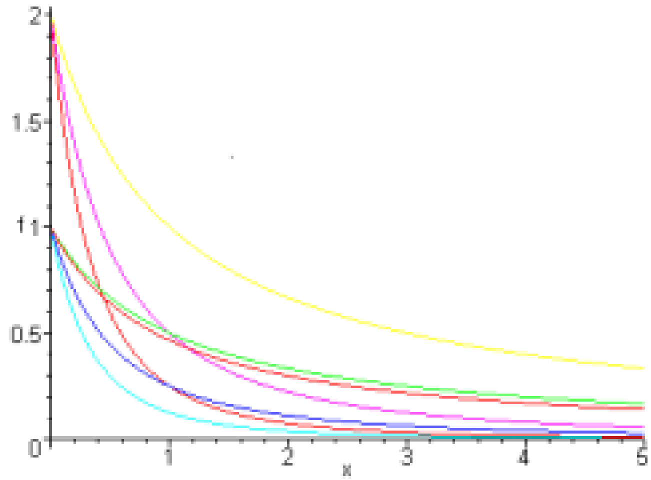


Figure 1:

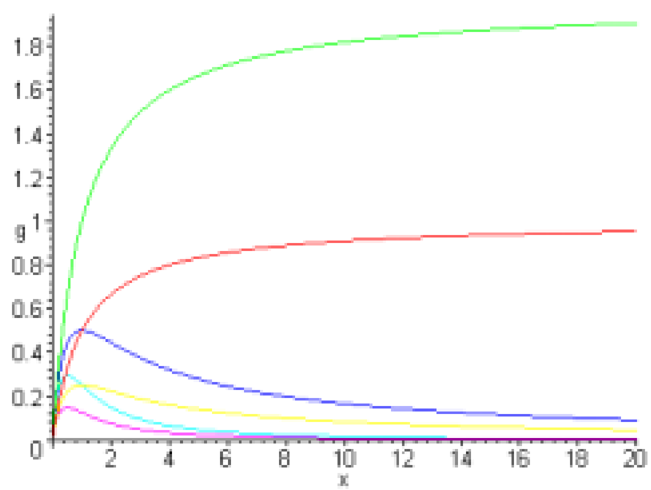


Figure 2:

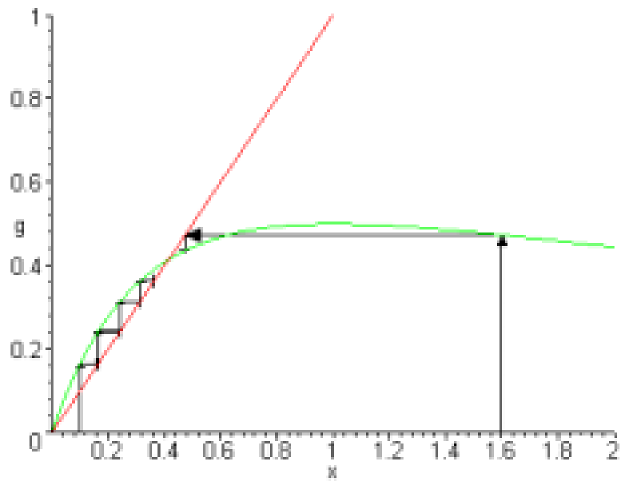


Figure 3:

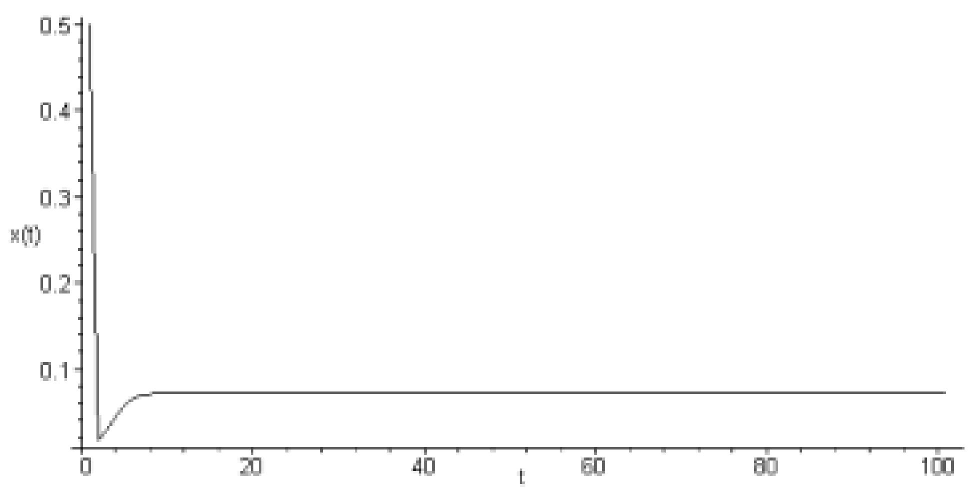


Figure 4:

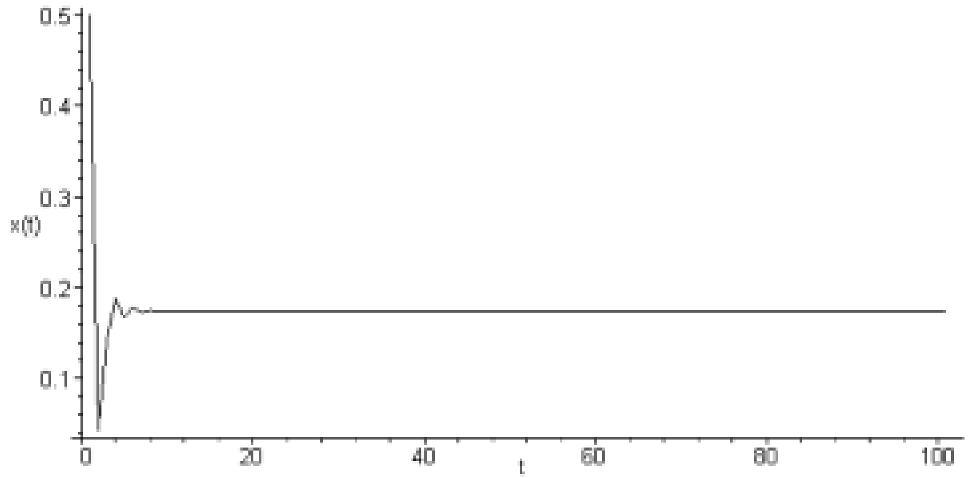
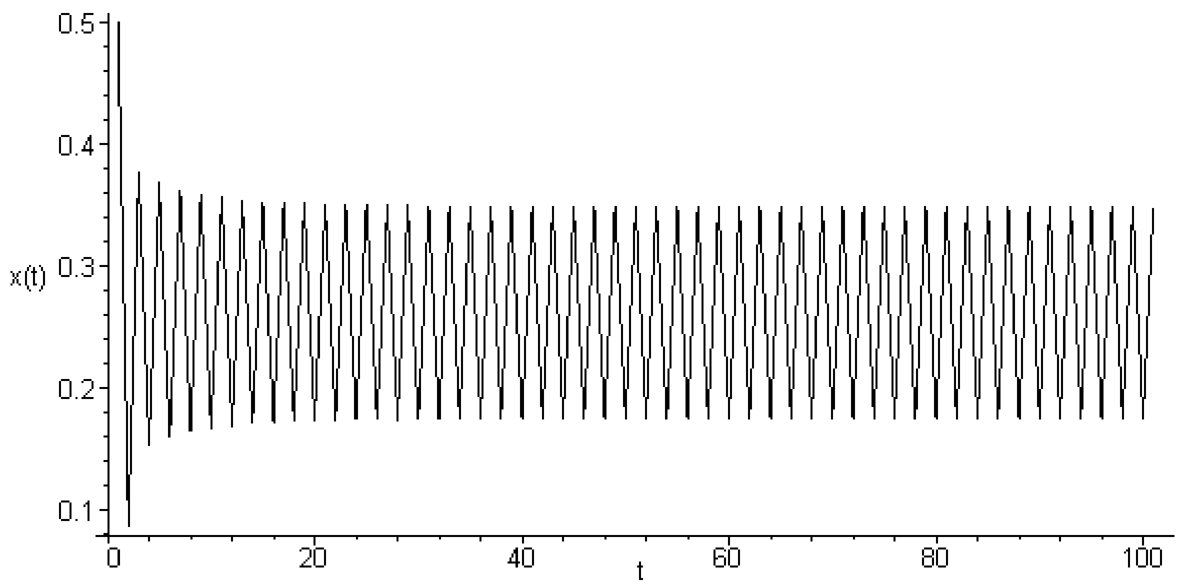


Figure 5:



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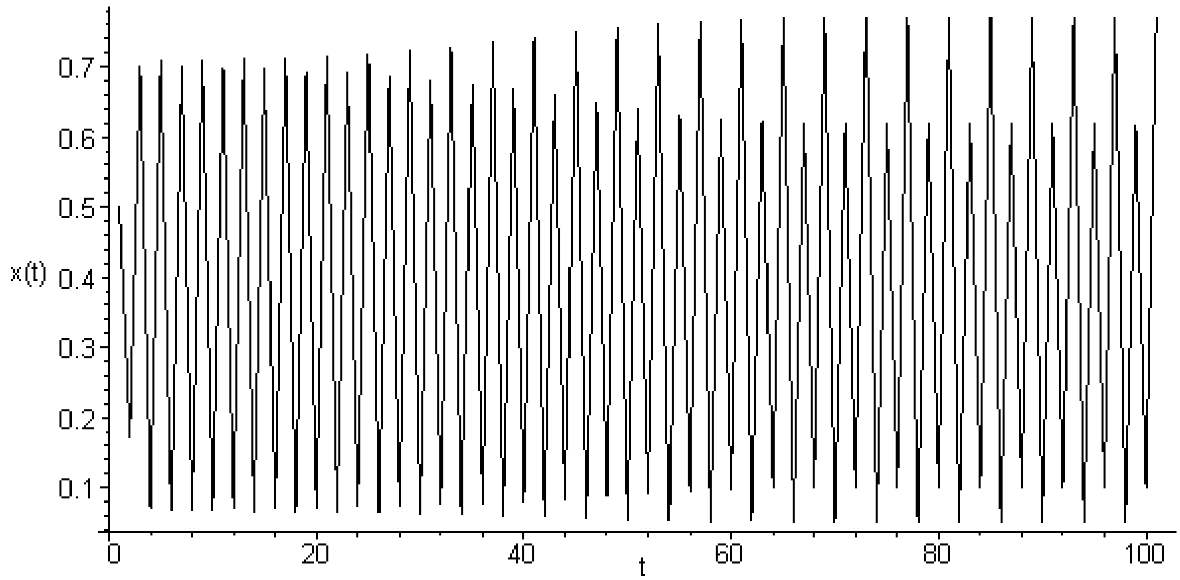

Figure 7:

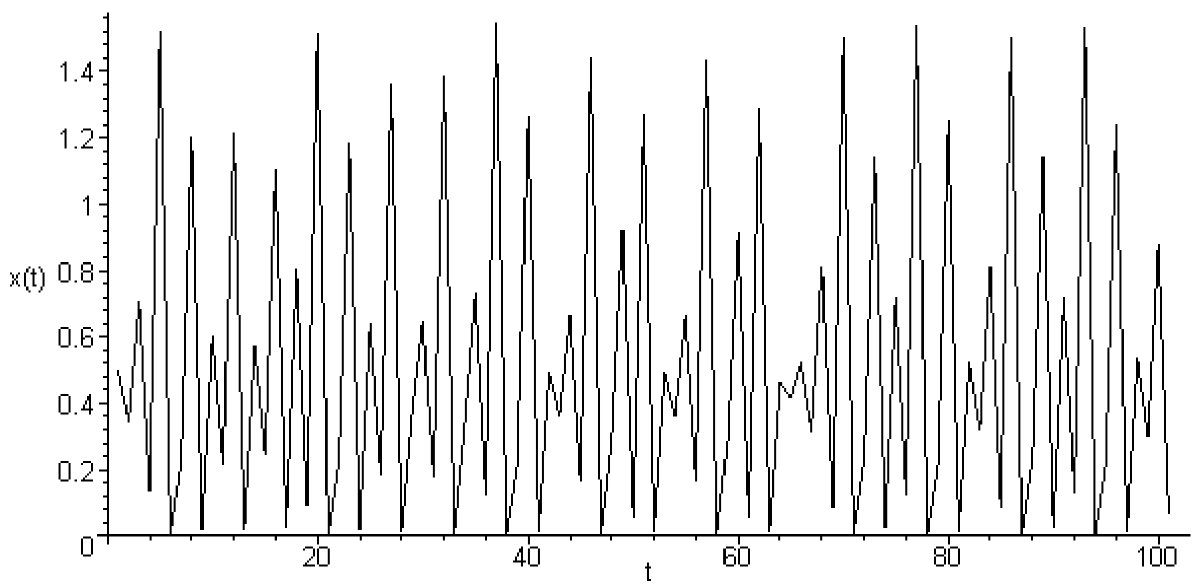

Figure 8:

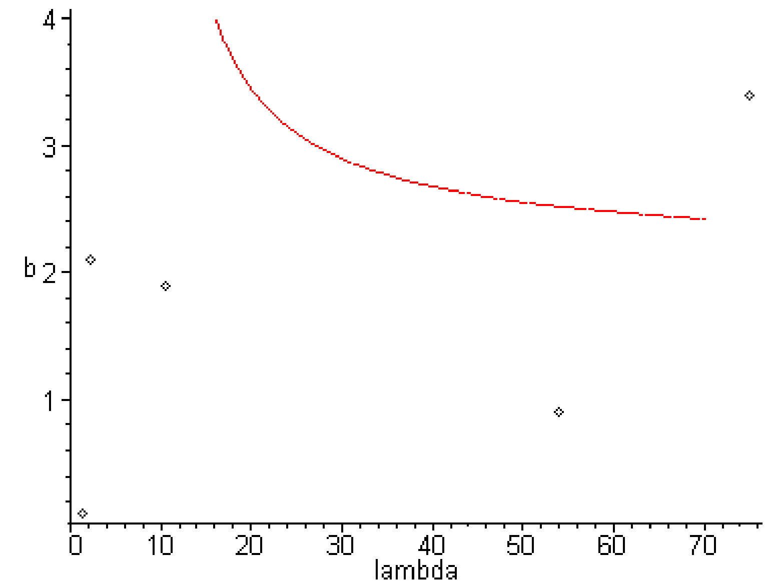

Figure 9:

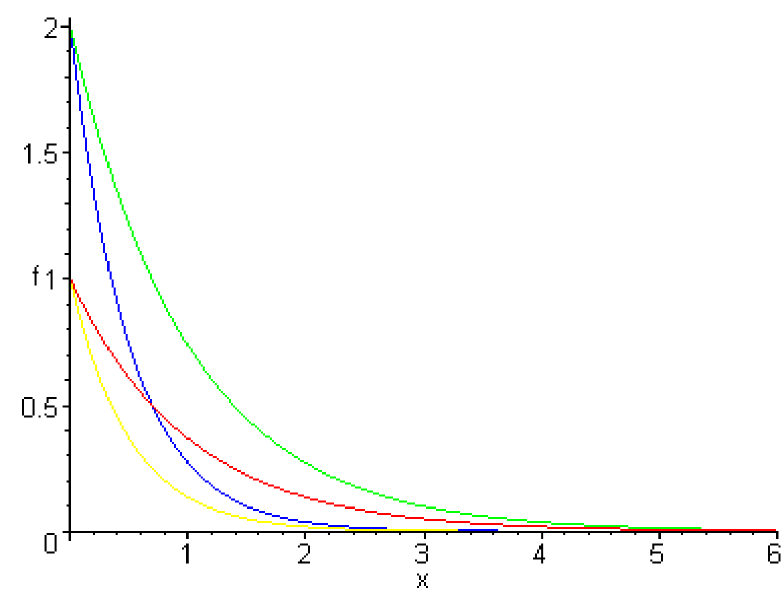

Figure 10:

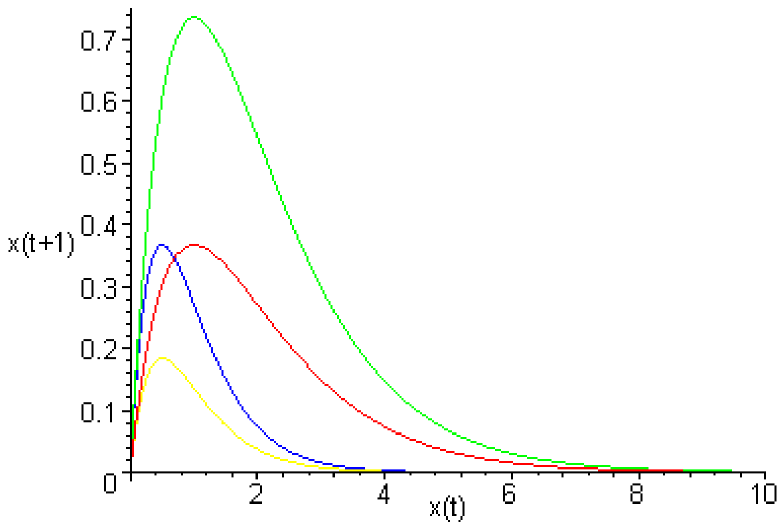

Figure 11:

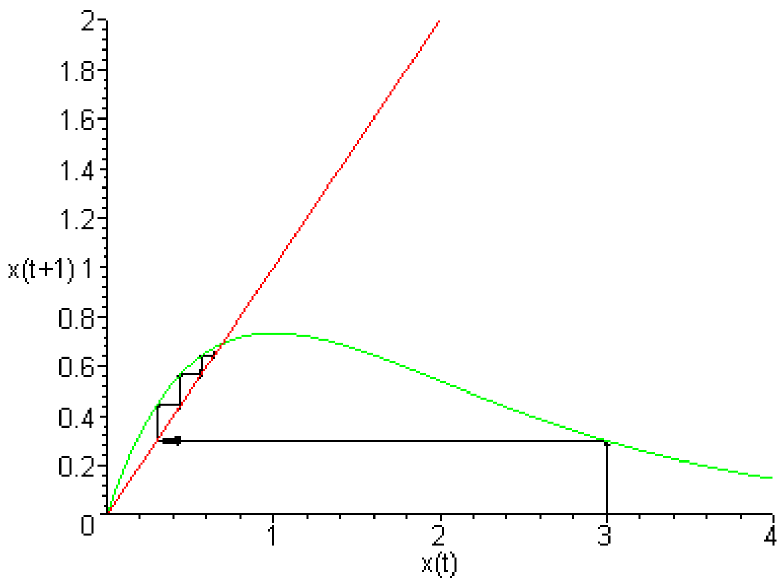

Figure 12: