

1.4 Exercises for Modeling

Exercise 1.4.1: Discrete-time versus continuous-time models

- (a) $\Delta t = 10$ minutes, and the probability of one cell making one other cell in 10 minutes is $p = 1$, since we are told that each cell effectively makes one copy of itself every 10 minutes.
- (b) Letting $N(t)$ be the population at time t , we have:

$$\begin{aligned} N(t + \Delta t) &= N(t) + pN(t) \\ &= N(t) + N(t) \\ &= 2N(t) \end{aligned} \tag{1.1}$$

We can see that the whole population doubles every 10 minutes.

- (c) We can define $\alpha := \frac{p}{\Delta t}$ (in this case, $\alpha = \frac{1}{10} \text{min}^{-1}$), and we can change our discrete model. Dividing (1.1) by Δt , we get:

$$\begin{aligned} \frac{N(t + \Delta t)}{\Delta t} &= \frac{N(t)}{\Delta t} + \frac{p}{\Delta t} N(t) = \frac{N(t)}{\Delta t} + \alpha N(t) \\ \Rightarrow \frac{N(t + \Delta t) - N(t)}{\Delta t} &= \alpha N(t) \end{aligned}$$

If we take the limit as $\Delta t \rightarrow 0$, we obtain the continuous model:

$$\frac{d}{dt} N(t) = \alpha N(t)$$

Exercise 1.4.2: Comparison of discrete and continuous models

Solution not available.

Exercise 1.4.3: Structured populations

Solution not available.

2.4 Exercises for Discrete-Time Models

Exercise 2.4.1: German population

Let x_n = Germany's population at the end of year n . The simplest model incorporating the given information is

$$\begin{aligned} x_{n+1} &= x_n - \delta x_n + \mu x_n \\ &= (1 - \delta + \mu)x_n \\ &= r x_n, \end{aligned} \tag{2.2}$$

where $r = 1 - \delta + \mu$.

At the end of the year 1998, we have $x_{1998} = 82,037,000$, and

$$\mu x_{1998} = 770,744, \quad \text{and} \quad \delta x_{1998} = 846,330,$$

which gives the values of μ and δ to be:

$$\begin{cases} \mu &= \frac{770,744}{82,037,000} = 0.009395, \\ \delta &= \frac{846,330}{82,037,000} = 0.010316, \end{cases} \tag{2.3}$$

and hence $r = 1 - 0.010316 + 0.009395 = 0.999079 < 1$. That is, the population will decay.

To make the model more realistic, we could add in terms for immigration and emigration, and use a logistic equation.

Exercise 2.4.2: Drug prescriptions

- (a) The dimensionless parameter k represents the fraction of the drug's dose which is used up or broken down by the body. The amount of the drug in a dose is represented by b . We know that $b \geq 0$ (no negative doses), and $k > 0$ (the body must use up *some* of the drug). Notice that if $b = 0$, then $a_{n+1} = a_n - k a_n$, so we better have $k \leq 1$ to avoid negative amounts. Summarizing the conditions on k and b ,

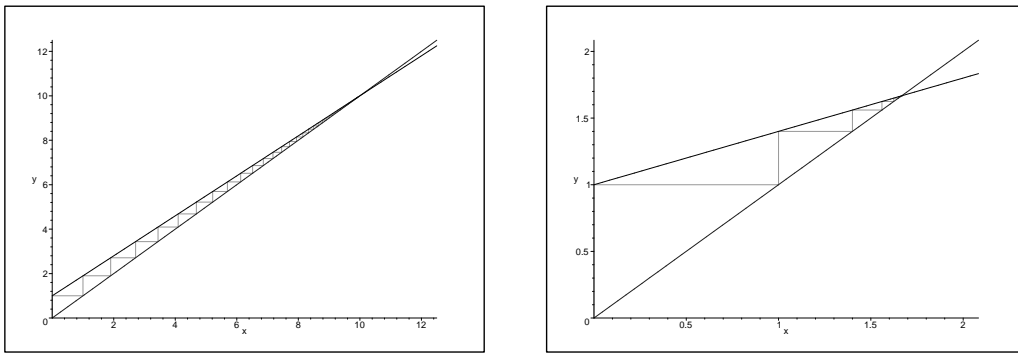
$$k \in (0, 1],$$

and

$$b \geq 0.$$

- (b) The fixed point (we know there is only one, since it is a linear equation), \bar{a} , of this model can be found if we let $f(x) := x - kx + b$, and solve for $f(\bar{a}) = \bar{a}$. This gives us $\bar{a} = b/k$. Further, $f'(x) = 1 - k$. We found in part (a) that $k \in (0, 1]$, so that means that $f'(x) \in [0, 1)$, which means that this fixed point, $\bar{a} = b/k$, is stable.

(c) In every case, we will start with the initial value of 0 (representing no dose given yet). Looking at the cobweb diagrams below, we can see that the map always settles down to the fixed point. The drug will have a constant concentration after sufficient time has passed, unless the dose is changed. The fixed point is reached more quickly if k is larger. In the figure below on the left, we have $k = 0.1$, and we can see many steps leading up to the fixed point. In the figure on the right, we set $k = 0.6$, and it takes fewer iterations of the map to reach the fixed point. Note that in these figures, we have set $b = 1$. Also, a larger value of k gives a smaller actual value of the fixed point. Since the fixed point is $\bar{a} = b/k$, we see that b behaves like a scaling factor, simply changing the value, but not the quality of the fixed point.



(d) We assume that there is a minimum amount, E , for which the drug will be effective, and a maximum amount, T , for which the drug becomes toxic. To make sure the drug is effective but not toxic, we need the fixed point to be between the values E and T :

$$E \leq \bar{a} < T$$

Substituting in for \bar{a} (found in part (b)), and multiplying through by k , we need the dosage b to be between the values kE and kT :

$$kE \leq b < kT.$$

Exercise 2.4.3: Improving the fit of the logistic model to the data

Solution not available.

Exercise 2.4.4: Fluctuations in the population of *P. aurelia*

Solution not available.

Exercise 2.4.5: Whale population

(a) The given equation,

$$a_{n+1} = a_n + k(M - a_n)(a_n - m),$$

describes the population of whales next year in terms of the population this year. The last term describes the change in the population, which is dependent on the 3 parameters, k , M , and m , with $m < M$.

- If $0 < a_n < m$, then $k(M - a_n)(a_n - m) < 0$, so the population will decline (specifically, the population next year is smaller than the population this year).
- If $m < a_n < M$, then $k(M - a_n)(a_n - m) > 0$, so the population will grow.
- If $a_n > M$, then $k(M - a_n)(a_n - m) < 0$, so the population will decline.
- If $a_n = m$ or $a_n = M$, then $k(M - a_n)(a_n - m) = 0$, so the population will remain the same size (that is, m and M are fixed points of the model).

(b) For fixed points \bar{a} , we require

$$\begin{aligned} \bar{a} &= \bar{a} + 0.0001(5000 - \bar{a})(\bar{a} - 100) \\ \iff 0.0001(5000 - \bar{a})(\bar{a} - 100) &= 0 \\ \iff \bar{a} = M = 5000 \quad \text{or} \quad \bar{a} = m = 100. \end{aligned}$$

To determine their stability, we let

$$\begin{aligned} f(x) &= x + 0.0001(5000 - x)(x - 100) \\ &= x + 0.0001(5000x - 500000 - x^2 + 100x) \\ &= x + 0.0001(5100x - 500000 - x^2). \end{aligned}$$

Then

$$f'(x) = 1 + 0.0001(5100 - 2x).$$

For the fixed point $\bar{a} = m = 100$, we have

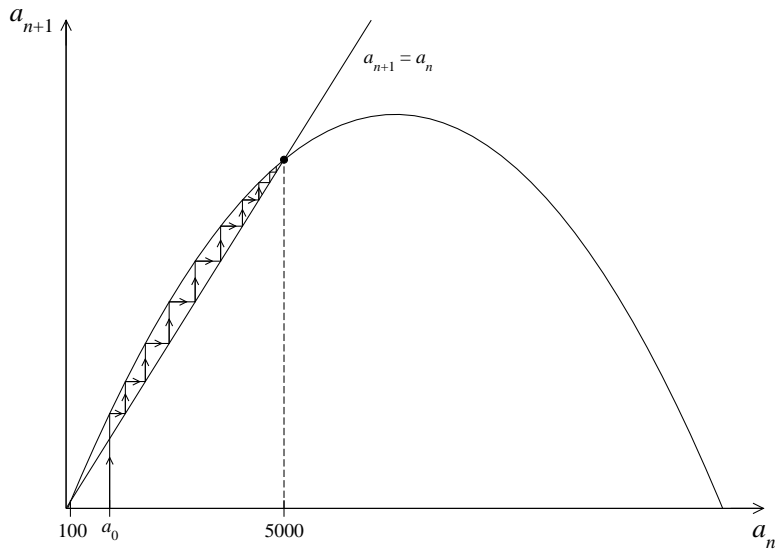
$$\begin{aligned} f'(100) &= 1 + 0.0001(5100 - 200) \\ &= 1.49 > 1, \end{aligned}$$

therefore $\bar{a} = m = 100$ is *unstable*. For the fixed point $\bar{a} = M = 5000$ we have

$$\begin{aligned} f'(5000) &= 1 + 0.0001(5100 - 10000) \\ &= 0.51 < 1 \quad (\text{but greater than } -1), \end{aligned}$$

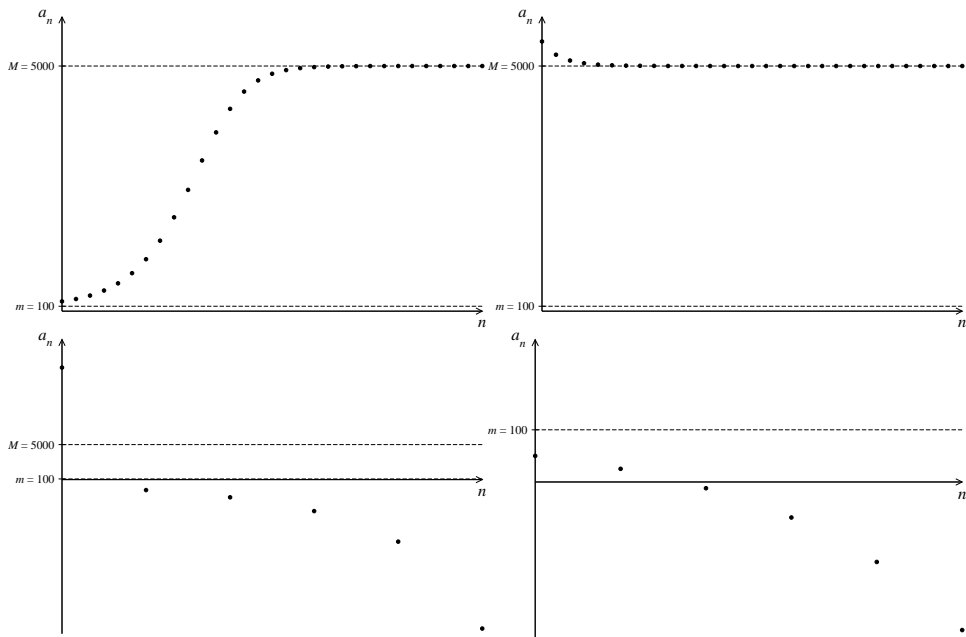
therefore $\bar{a} = M = 5000$ is *stable*.

(c)



As before, we conclude that $\bar{a} = m = 100$ is unstable, and $\bar{a} = M = 5000$ is stable.

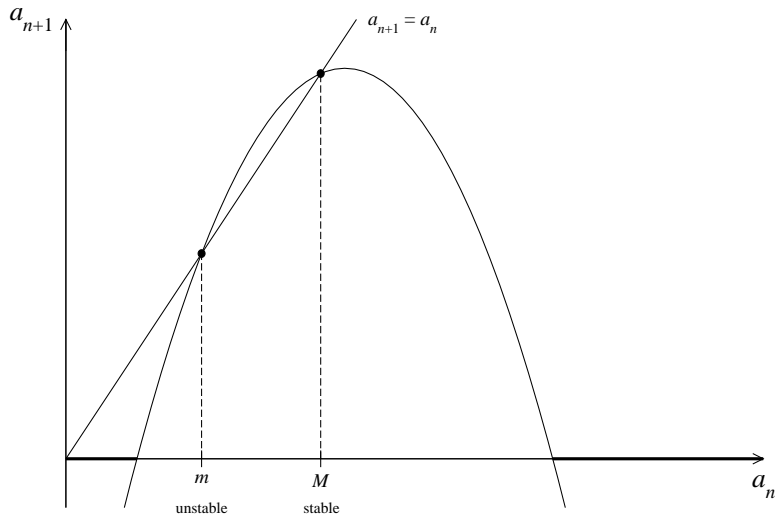
(d)



(e) When $a_0 < m$, the population declines, eventually becoming negative. When $a_0 \gg M$ (i.e., when a_0 is greater than the biggest root of the map), then

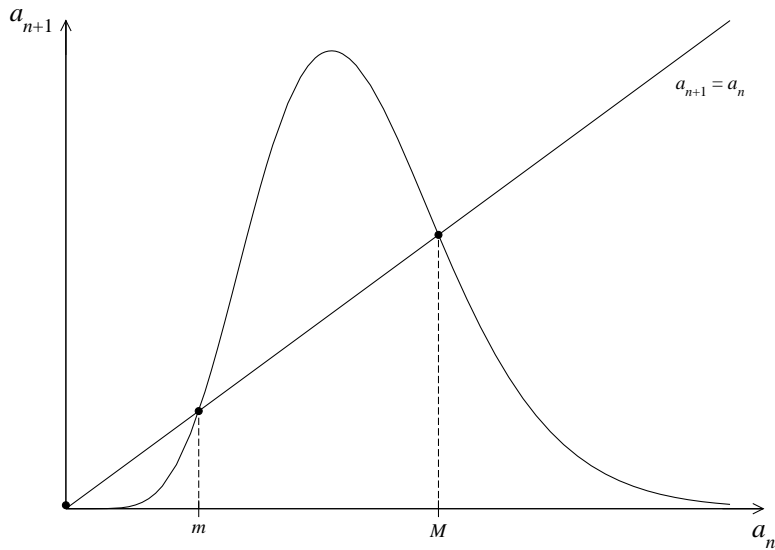
$a_1 < 0$, and the population continues to decline. Both cases are problematic, since it is non-sensical to have a negative number of whales.

- (f) If we plot a_{n+1} versus a_n for the given model, we obtain the following qualitative graph:



We see that if the whale population ever reaches a value located on the highlighted (thick) portions of the a_n -axis, the population will be negative next year, since the graph of a_{n+1} versus a_n lies below the a_n -axis there.

To fix the problem, we could ensure that the graph of a_{n+1} versus a_n always lies above the a_n -axis. For example:



Exercise 2.4.6: Second-iterate map

(a)

$$\begin{aligned} f^2(x) &= r(rx(1-x))(1-(rx(1-x))) \\ &= r^2x(1-(r+1)x+2rx^2-rx^3) \end{aligned}$$

- (b) We already know the fixed points of f . Since they are fixed points of f , they also are fixed points of f^2 . These two “trivial 2-cycles” are $x = 0$ and $x = \frac{r-1}{r}$. Since we know they are fixed points of f^2 , i.e., we know they satisfy $f^2(x) = x$, we know that they are solutions of $f^2(x) - x = 0$. This means we can rewrite $f^2(x) - x$ as $x(x - \frac{r-1}{r})q(x)$, where $q(x)$ is an unknown quadratic polynomial. We then set this new expression equal to what we know for $f^2(x) - x$:

$$x(x - \frac{r-1}{r})q(x) = r^2x(1 - (r+1)x + 2rx^2 - rx^3) - x.$$

Since we are interested in nonzero solutions, we can drop the common x factor on each side. We don't want the $(r-1)/r$ root either, so we can drop that, by dividing both sides by $x - \frac{r-1}{r}$. Hence,

$$q(x) = \frac{r^2(1 - (r+1)x + 2rx^2 - rx^3) - 1}{x - \frac{r-1}{r}}.$$

Carrying out the long division, we end up with

$$q(x) = -r^3x^2 + (r^3 + r^2)x - r^2 - r.$$

The roots of this polynomial are the last two roots of f^2 . Now we can find them by simply invoking the quadratic formula:

$$x = \frac{-(r^3 + r^2) \pm \sqrt{(r^3 + r^2)^2 - 4r^3(r^2 - r)}}{-2r^3}.$$

This can be simplified to

$$x = \frac{r+1 \pm \sqrt{(r-3)(r+1)}}{2r}.$$

It is these two roots we are interested in, because the first two are trivial 2-cycles. Recall the restriction of $r \in [0, 4]$ which was discussed in section (later), so the term $(r+1)$ in the radical poses no problem for us. It is the $(r-3)$ term which tells us when this 2-cycle exists. Obviously, this 2-cycle does *not* exist if $r < 3$ (imaginary roots). If $r = 3$, this ceases to be a 2-cycle, because the roots which make up the 2-cycle become the same (the radical evaluates to zero). Hence, a nontrivial 2-cycle exists only for $r > 3$.

(c) After a bit of simplification, we find that

$$\frac{d}{dx}f^2(x) = -4r^3x^3 + 6r^3x^2 - 2(r^2 + r^3)x + r^2.$$

(d) This can be done with a few MAPLE commands. One is complicated. What we want to do is turn the derivative, with the fixed points substituted in already, into a function of r :

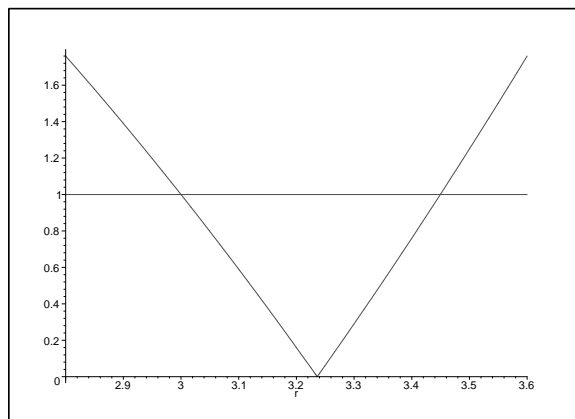
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> d:=q-> subs( r=q, abs( subs( x=sol[3], diff(f2(x), x)
) ) ):

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The explanation of this command is as follows (from the inside out):

We substitute the 3rd solution that MAPLE gave for the fixed points of $f^2(x)$ into the derivative of $f^2(x)$, and then take the absolute value. We make it a function by replacing the r 's that appear with the dummy variable, q , which we are using to define the function in terms of. Now if we call $d(r_0)$, it will give us the absolute value of the derivative of f^2 at the fixed point with $r = r_0$.

Next, we want to plot $d(r)$, between 2.8 and 3.6 (to include the points 3 and $1 + \sqrt{6} \approx 3.449$). A horizontal line has been added to see where the graph crosses $d(r) = 1$.



Looking at this, we can see that d is above 1 for $r < 3$ and below 1 for $r > r^*$, where $r^* \approx 3.5$. This means that the 2-cycle is unstable and stable in those regions, respectively. To find the exact values at which the stability changes, we use the solve command:

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> solve(d(r)=1, r);
```

$$1 + \sqrt{6}, 1 - \sqrt{6}, 3, -1$$

Hence, the 2-cycle is stable for $3 < r < 1 + \sqrt{6}$ and unstable for $r > 1 + \sqrt{6}$. Note that $1 + \sqrt{6} \approx 3.449$, confirming our observation from the graph above.

Exercise 2.4.7: Fourth-iterate map

Solution not available.

Exercise 2.4.8: Exact solution for the Beverton-Holt model

We have

$$x_{n+1} = \frac{r}{1 + \frac{r-1}{K} x_n} x_n$$

Let $u_n = \frac{1}{x_n}$. Then

$$\begin{aligned} \frac{1}{u_{n+1}} &= \frac{r}{1 + \frac{r-1}{K} \frac{1}{u_n}} \frac{1}{u_n} \\ u_{n+1} &= \frac{1}{r} \left(1 + \frac{r-1}{K} \frac{1}{u_n} \right) u_n \\ &= \frac{1}{r} u_n + \frac{r-1}{rK} \end{aligned}$$

This equation is linear, of the form

$$u_{n+1} = Au_n + B,$$

where $A = \frac{1}{r}$ and $B = \frac{r-1}{rK}$.

We can find a solution to this equation as follows:

$$\begin{aligned} u_{n+1} &= Au_n + B \\ &= A[Au_{n-1} + B] + B \\ &= A^2u_{n-1} + B(A + 1) \\ &= A^2[Au_{n-2} + B] + B(A + 1) \\ &= A^3u_{n-2} + B(A^2 + A + 1) \\ &\vdots \\ &= A^{n+1}u_0 + B(A^n + A^{n-1} + \dots + A + 1) \\ &= A^{n+1}u_0 + B \frac{A^{n+1} - 1}{A - 1} \end{aligned}$$

Returning to the original variables, we have

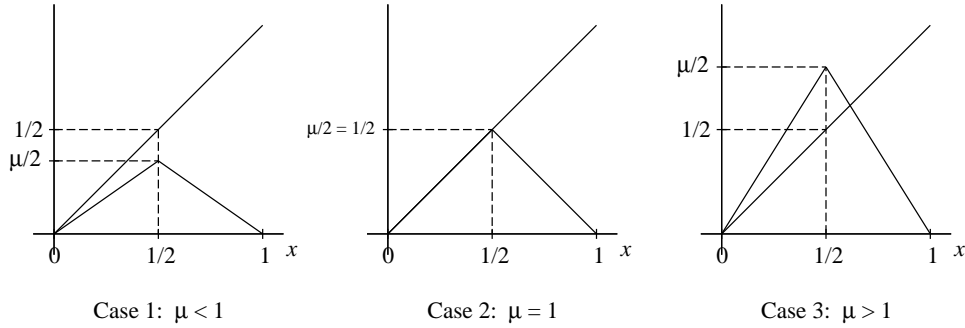
$$\begin{aligned} \frac{1}{x_{n+1}} &= \frac{1}{r^{n+1}} \frac{1}{x_0} + \frac{r-1}{rK} \frac{\frac{1}{r^{n+1}} - 1}{\frac{1}{r} - 1} \\ &= \frac{1}{x_0 r^{n+1}} + \frac{r^{n+1} - 1}{r^{n+1} K} \\ &= \frac{K + x_0(r^{n+1} - 1)}{x_0 K r^{n+1}} \\ x_{n+1} &= \frac{r^{n+1} x_0}{1 + \frac{x_0}{K}(r^{n+1} - 1)} \end{aligned}$$

Exercise 2.4.9: Fitting the Beverton-Holt model to Gause’s data

Solution not available.

Exercise 2.4.10: The tent map

- (a) We distinguish three cases: Case 1: $\mu < 1$, Case 2: $\mu = 1$, Case 3: $\mu > 1$.
Graphs of f are:



- (b) In case 1, there is one fixed point, $\bar{x} = 0$. In case 2, there are infinitely many fixed points $0 \leq \bar{x} \leq \frac{1}{2}$. In case 3, there are two fixed points, $\bar{x}_1 = 0$ and $\bar{x}_2 = \frac{\mu}{1+\mu}$.

To determine their stability, we look at the derivative of $f(x)$ at each of the fixed points:

$$f'(x) = \begin{cases} \mu & \text{for } 0 \leq x < 0.5 \\ -\mu & \text{for } 0.5 < x \leq 1 \end{cases}$$

In case 1, $f'(0) = \mu < 1$, therefore $\bar{x} = 0$ is stable. In case 2, $f'(\bar{x}) = \mu = 1$, and the stability of these fixed points is undetermined. In case 3, $f'(0) = \mu > 1$, therefore $\bar{x}_1 = 0$ is unstable. Similarly, $f'(\frac{\mu}{1+\mu}) = -\mu < -1$, and so $\bar{x}_2 = \frac{\mu}{1+\mu}$ is unstable as well.

- (c) We’ll define two functions, $f_1(x) = \mu x$, and $f_2(x) = \mu(1-x)$, and loosely define the terms “the first region” and “the second region” to mean $\{x : 0 \leq x < 0.5\}$, and $\{x : 0.5 < x \leq 1\}$, respectively. There are three possibilities for any 2-cycle in this situation, namely that both iterates lie in the first region, they both lie in the second region, or one lies in the first region and the second in the second region (there’s really one more with the opposite condition of the last one, but this one can be found by simply applying f to the one found in the last case, and those are the two iterates of the same 2-cycle). To find 2-cycles, we set $\bar{x} = f(f(\bar{x}))$.

- Case (i): Both lie in the first region. Then $f(f(x)) = f_1^2(x) = \mu(\mu x) = \mu^2 x$, and the fixed point \bar{x} must satisfy

$$\bar{x} = \mu^2 \bar{x},$$

which has only the trivial solution, $\bar{x} = 0$, which we already know to be 1-cycle, so we are not interested in this case.

- Case (ii): Both lie in the second region. Then $f(f(x)) = f_2^2(x) = \mu(1 - [\mu(1 - x)]) = \mu - \mu^2 + \mu^2 x$. The fixed point must satisfy

$$\bar{x} = \mu - \mu^2 + \mu^2 \bar{x},$$

which has solution

$$\bar{x} = \frac{\mu(1 - \mu)}{(1 - \mu)(1 + \mu)} = \frac{\mu}{1 + \mu}.$$

Since \bar{x} must lie in the second region, we require $\mu > 1$. This is the same solution as for the 1-cycle, so again, we are not interested in this case.

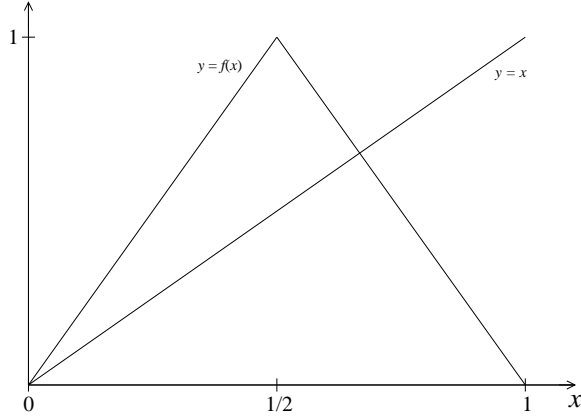
- Case (iii): The first lies in the first region, and the second lies in the second region. Here, applying f twice will give $f(f(x)) = f_2(f_1(x)) = \mu(1 - \mu x) = \mu - \mu^2 x$. The fixed point must satisfy

$$\bar{x} = \mu - \mu^2 \bar{x},$$

which has solution $\bar{x} = \mu/(1 + \mu^2)$. Note that this point lies in the first region no matter what μ is. The proof lies in the fact that for any $\mu \in \mathbb{R}$, we have $(\mu - 1)^2 \geq 0$. With a little rearranging, the inequality turns into $\mu/(\mu^2 + 1) \leq 1/2$, for all $\mu \in \mathbb{R}$. As described above, we can find the other orbit of this 2-cycle by applying f to \bar{x} . Renaming \bar{x} to p , the 2-cycle will be p and q , where $q = f(p) = \mu^2/(1 + \mu^2)$. Since we found this 2-cycle by assuming that the first iterate is in the first region (which it is) and the second is in the second region, we must restrict μ such that q is in the second region. That is, we need to make sure that $1/2 < \mu^2/(\mu^2 + 1) \leq 1$. The right-hand side of the inequality is trivial, but the left-hand side forces us to put $\mu > 1$ (keeping in mind that $\mu > 0$). Therefore, a nontrivial 2-cycle exists only for $\mu > 1$, and it is:

$$\left\{ p = \frac{\mu}{\mu^2 + 1}, \quad q = \frac{\mu^2}{\mu^2 + 1} \right\}.$$

(d)



As in (c), we think of the different cases of where the iterates of a 3-cycle could reside. There seem to be eight possibilities. We denote each possibility with a 3-tuple, where 1 means “the iterate lies in the first region”, and 2 means “the iterate lies in the second region”. The eight possibilities thus are

- (1, 1, 1),
- (1, 1, 2),
- (1, 2, 1),
- (1, 2, 2),
- (2, 1, 1),
- (2, 1, 2),
- (2, 2, 1),
- (2, 2, 2).

Since a 3-cycle is literally a cycle, any cyclic permutation of the above 3-tuples will be the same 3-cycle (it doesn’t matter which is the “first” iterate of the three, the important thing is the order of the three). This means that we have some repetition in the above list, for example (2, 1, 1) is the same as (1, 1, 2), which is the same as (1, 2, 1). Eliminating the repeated ones, we obtain the following four essential cases:

- Case (i) : (1, 1, 1),
- Case (ii) : (1, 1, 2),
- Case (iii) : (1, 2, 2),
- Case (iv) : (2, 2, 2).

To find a first point of a 3-cycle, we need $\bar{x} = f(f(f(\bar{x})))$.

- Case (i): All of the iterates of our 3-cycle lie in the first region. If this is the case, then the equation we get for the fixed point \bar{x} of the third-iterate function is (remember that $\mu = 2$ in this problem)

$$\bar{x} = f^3(\bar{x}) = f_1^3(\bar{x}) = \mu^3 \bar{x} = 8\bar{x}.$$

As in part (c), we have the 1-cycle $\bar{x} = 0$ again, so this is a trivial 3-cycle.

- Case (ii): The first two iterates are in the first region and the third is in the second region. Now we would have for \bar{x} :

$$\bar{x} = f^3(\bar{x}) = f_2(f_1(f_1(\bar{x}))) = f_2(f_1(2\bar{x})) = f_2(4\bar{x}) = 2(1 - 4\bar{x}) = 2 - 8\bar{x}.$$

Hence the fixed point of the third-iterate function is $\bar{x} = 2/9$. We can find the rest of this 3-cycle by applying f to this point, and applying f again. Let $p = 2/9$, and then q and r will be the other two iterates of the 3-cycle. $q = f(p) = f(2/9) = f_1(2/9) = 2 \cdot 2/9 = 4/9$, and then $r = f(q) = f(4/9) = f_1(4/9) = 2 \cdot 4/9 = 8/9$. We can check that $p = f(r)$: $f(r) = f(8/9) = f_2(8/9) = 2(1 - 8/9) = 2/9 = p$, as expected. Hence, our 3-cycle is

$$\left\{ p = \frac{2}{9}, \quad q = \frac{4}{9}, \quad r = \frac{8}{9} \right\}.$$

We could stop here, since the question asks to find an orbit of period 3 (i.e., a 3-cycle), but we'll continue to check the cases, in case we can find another one.

- Case (iii): The first iterate lies in the first region, and the other two are in the second region. Our equation for the fixed point of $f^3(x)$ is then

$$\begin{aligned} \bar{x} = f^3(\bar{x}) &= f_2(f_2(f_1(\bar{x}))) = f_2(f_2(2\bar{x})) = f_2(2(1 - 2\bar{x})) \\ &= f_2(2 - 4\bar{x}) = 2(1 - (2 - 4\bar{x})) = 2 - 4 + 8\bar{x} \\ &= -2 + 8\bar{x}. \end{aligned}$$

This time we get $\bar{x} = 2/7$. Doing the same thing as for case (ii), we put $p = 2/7$, and then $q = f(p) = f(2/7) = f_1(2/7) = 2 \cdot 2/7 = 4/7$, and $r = f(q) = f(4/7) = f_2(4/7) = 2(1 - 4/7) = 2 \cdot 3/7 = 6/7$. We check the solution by finding $f(r) = f(6/7) = f_2(6/7) = 2(1 - 6/7) = 2 \cdot 1/7 = 2/7$, and we see that this is correct. Hence, another 3-cycle is

$$\left\{ p = \frac{2}{7}, \quad q = \frac{4}{7}, \quad r = \frac{6}{7} \right\}.$$

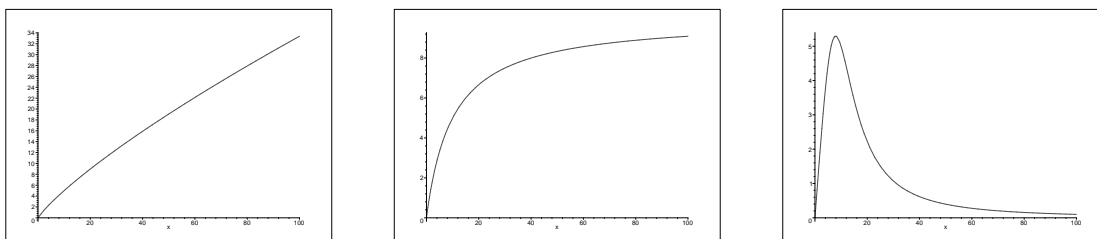
- Case (iv): All iterates of the 3-cycle are in the second region. Then the equation for a fixed point of $f^3(x)$ is

$$\begin{aligned} \bar{x} = f^3(\bar{x}) &= f_2^3(\bar{x}) = f_2(f_2(2(1 - \bar{x}))) = f_2(f_2(2 - 2\bar{x})) = f_2(2(1 - (2 - 2\bar{x}))) \\ &= f_2(2 - 4 + 4\bar{x}) = f_2(-2 + 4\bar{x}) = 2(1 - (-2 + 4\bar{x})) = 2(3 - 4\bar{x}) \\ &= 6 - 8\bar{x}. \end{aligned}$$

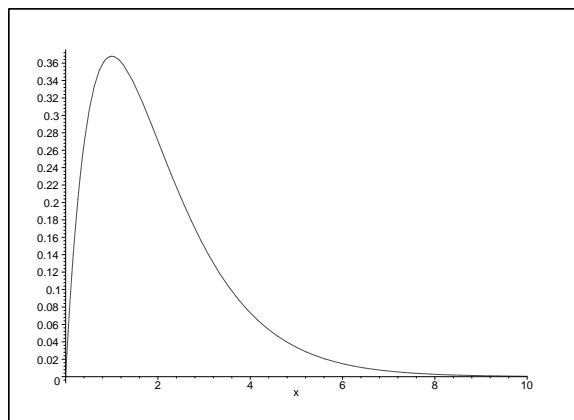
This gives us the solution $\bar{x} = 2/3$. Again, we set $p = 2/3$, and let $q = f(2/3) = f_2(2/3) = 2(1 - 2/3) = 2/3$. We need not go any further, because we can see that this is a 1-cycle, a trivial 3-cycle. This is the 1-cycle we found in part (b), with $\mu = 2$ (we can verify: $\mu/(1 + \mu) = 2/(1 + 2) = 2/3$).

Exercise 2.4.11: Blood cell population

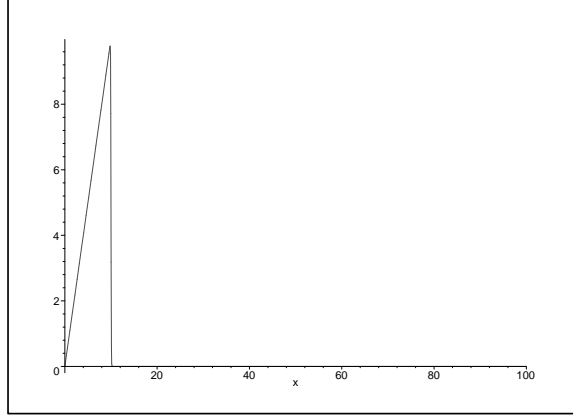
- (a) First we graph the function on Maple for the three cases of m : $m < 1$, $m = 1$, and $m > 1$, for a fixed θ :



For $m < 1$, $p_2(x) \rightarrow \infty$ as $x \rightarrow \infty$. For $m = 1$, $p_2(x)$ approaches $b\theta$ for $x \rightarrow \infty$. If $m > 1$, then $p_2(x)$ will go to zero as $x \rightarrow \infty$. It is actually this case where $p_2(x)$ takes the shape of $p_1(x)$. The graph of $p_1(x)$ is shown below, with $a = 1$ and $b = 1$.



If we look at the case $m \gg 1$, we see that the peak gets sharper. In the limit of $m \rightarrow \infty$ the graph looks linear with a sudden drop to zero, as shown below.



Changing the value of θ causes the horizontal scale to change, but does not affect the shape of the curve. Large θ gives larger $p_2(x)$ at larger x . Finally, changing the value of b simply changes the vertical scale.

- (b) Assume it is q days that red blood cell production is delayed. Then instead of the original model,

$$x_{n+1} = x_n - d(x_n) + p(x_n),$$

we take the number of cells gained q days earlier, so the model becomes

$$x_{n+1} = x_n - d(x_n) + p(x_{n-q}).$$

Exercise 2.4.12: Population genetics

Solution not available.

Exercise 2.4.13: Competition

Solution not available.

Exercise 2.4.14: Spread of infectious disease

- (a) For fixed points \bar{I} , we require

$$\begin{aligned} \bar{I} &= \bar{I} + k\bar{I}(N - \bar{I}) \\ \iff k\bar{I}(N - \bar{I}) &= 0 \\ \iff \bar{I} = 0 \quad \text{or} \quad \bar{I} &= N. \end{aligned}$$

To determine the stability of the fixed points, we let

$$f(I) = (1 + kN)I - kI^2.$$

Differentiating gives

$$f'(I) = 1 + kN - 2kI.$$

Since

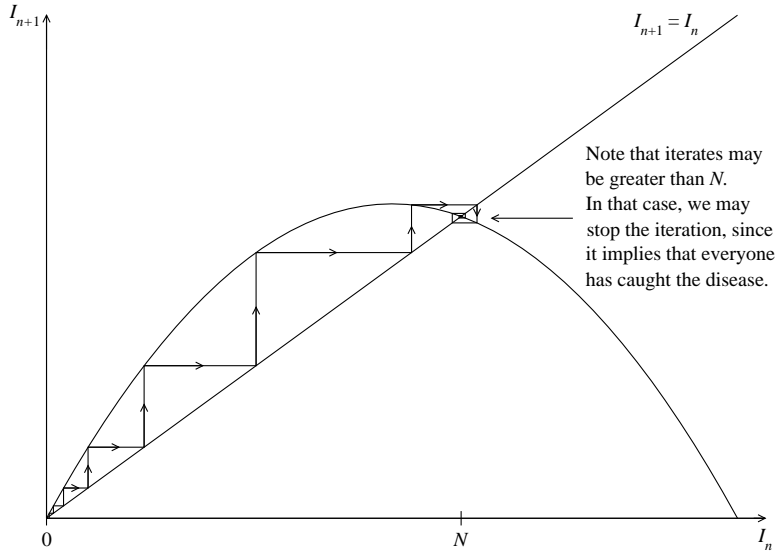
$$f'(0) = 1 + kN > 1,$$

the trivial fixed point $\bar{I} = 0$ is *unstable*. The stability of the nontrivial fixed point $\bar{I} = N$ is given by

$$f'(N) = 1 + kN - 2kN = 1 - kN.$$

Since $kN < 2$, we have $-1 < 1 - kN < 1$, and therefore $\bar{I} = N$ is *stable*.

Cobwebbing gives the following picture:



The model predicts that as time progresses, *everyone* catches the disease.

- (b) We introduce a new class of individuals, namely those who have been ill, but now have recovered with immunity. Let the number of such individuals on day n be R_n . Then the number of newly infected individuals on day $n + 1$ is

$$\underbrace{k I_n}_{\text{people who are sick}} \underbrace{(N - I_n - R_n)}_{\text{people available to catch disease}}.$$

The number of people who move from the infected to the recovered class on day n are those that became newly infected d days ago. That is,

$$kI_{n-d} (N - I_{n-d} - R_{n-d}).$$

Putting things together, we obtain

$$\begin{cases} I_{n+1} &= I_n + kI_n(N - I_n - R_n) - kI_{n-d} (N - I_{n-d} - R_{n-d}) \\ R_{n+1} &= R_n + kI_{n-d} (N - I_{n-d} - R_{n-d}). \end{cases}$$

with

$$\begin{aligned} I_{-d} &= \cdots = I_{-2} = I_{-1} = 0 \\ I_0 &= 1 \\ R_{-d} &= \cdots = R_{-1} = R_0 = R_1 = \cdots = R_{d-1} = 0 \\ R_d &= 1 \end{aligned}$$

The additional assumption we made is that people remain sick for precisely d days. That is, all people who become ill at the same time recover at the same time.

Exercise 2.4.15: Jury conditions

We have

$$J = \begin{bmatrix} a_R & p_R \\ p_J & a_J \end{bmatrix}.$$

(a) The characteristic polynomial of J is

$$\begin{aligned} \det \begin{bmatrix} a_R - \lambda & p_R \\ p_J & a_J - \lambda \end{bmatrix} &= 0 \\ \iff (\lambda - a_R)(\lambda - a_J) - p_R p_J &= 0 \\ \iff \lambda^2 - (a_R + a_J)\lambda + a_R a_J - p_R p_J &= 0 \\ \iff \lambda^2 - \text{tr } J \lambda + \det J &= 0, \end{aligned}$$

as required.

(b) The eigenvalues of J are

$$\lambda = \frac{\beta \pm \sqrt{\beta^2 - 4\gamma}}{2},$$

where $\beta := \text{tr } J$ and $\gamma := \det J$.

Thus, we need to prove

$$|\beta| < 1 + \gamma < 2 \iff |\lambda| < 1. \tag{2.4}$$

We will show both directions of the implication separately.

“ \Rightarrow ”: Suppose the first part of (2.4) is satisfied. We then need to show that both eigenvalues will have magnitude less than 1. The form of the eigenvalues tells us that they could be complex with nonzero imaginary part. If this is the case, we know that the eigenvalues can be rewritten in the form

$$\lambda = \frac{\beta \pm i\sqrt{4\gamma - \beta^2}}{2}, \tag{2.5}$$

with $4\gamma > \beta^2$.

Thus, for complex eigenvalues,

$$|\lambda|^2 = \frac{\beta^2}{4} + \frac{4\gamma - \beta^2}{4} = \gamma < 1,$$

since $1 + \gamma < 2$ by assumption. Of course, once we have that $|\lambda|^2 < 1$, we get automatically that $|\lambda| < 1$.

Now that we have the complex case covered, we can assume $\beta^2 \geq 4\gamma$, so that the eigenvalues are real, and proceed the following way:

$$\begin{aligned} |\lambda| &= \left| \frac{\beta \pm \sqrt{\beta^2 - 4\gamma}}{2} \right| \\ &\leq \frac{|\beta|}{2} + \frac{|\sqrt{\beta^2 - 4\gamma}|}{2} \quad (\text{triangle inequality, regardless of the sign of the radical}) \\ &< \frac{1 + \gamma + |\sqrt{(1 + \gamma)^2 - 4\gamma}|}{2} \quad (\text{left-hand inequality relating } \beta \text{ and } \gamma) \\ &= \frac{1 + \gamma + |\sqrt{(1 - \gamma)^2}|}{2} \\ &= \frac{1 + \gamma + |1 - \gamma|}{2} \\ &= \frac{1 + \gamma + 1 - \gamma}{2} \quad (\text{since } \gamma < 1, |1 - \gamma| = 1 - \gamma) \\ &= 1. \end{aligned}$$

Therefore, $|\lambda| < 1$ for real or complex eigenvalues, and we have shown this direction of the implication.

“ \Leftarrow ”: Suppose now the right hand side of the implication in (2.4) is satisfied (that is, $|\lambda| < 1$ for both eigenvalues λ). We then need to show that $|\beta| < 1 + \gamma < 2$.

Again we will break this up into the cases of complex with nonzero imaginary part, and purely real eigenvalues.

First, if $\beta^2 < 4\gamma$, the eigenvalues will be complex and we'll get:

$$\begin{aligned} |\lambda| < 1 &\Rightarrow |\lambda|^2 < 1 \\ &\Rightarrow \frac{\beta^2}{4} + \frac{4\gamma - \beta^2}{4} < 1 \\ &\Rightarrow \gamma < 1 \\ &\Rightarrow 1 + \gamma < 2, \end{aligned}$$

which implies one of the Jury conditions. To show the other condition,

we start with

$$\begin{aligned}
 & \gamma^2 - 2\gamma + 1 > 0 \\
 & \Rightarrow \gamma^2 + 2\gamma + 1 > 4\gamma \\
 & \Rightarrow (\gamma + 1)^2 > 4\gamma \\
 & \Rightarrow (\gamma + 1)^2 > \beta^2 \quad (4\gamma > \beta^2, \text{ by assumption}) \\
 & \Rightarrow \gamma + 1 > |\beta|.
 \end{aligned}$$

Note that the last step is allowed because $4\gamma > \beta^2 \geq 0 \Rightarrow \gamma > -1$ (if $\gamma \leq -1$, we would need to put $|\gamma + 1| > |\beta|$). We have now shown the desired result in the case of complex eigenvalues when $4\gamma > \beta^2$.

In the real case, we substitute in for both of the eigenvalues in the inequality $|\lambda| < 1$:

$$\begin{cases} -1 < \frac{\beta + \sqrt{\beta^2 - 4\gamma}}{2} < 1, \\ -1 < \frac{\beta - \sqrt{\beta^2 - 4\gamma}}{2} < 1. \end{cases}$$

We can then isolate $\beta/2$:

$$\begin{cases} -1 - \frac{\sqrt{\beta^2 - 4\gamma}}{2} < \frac{\beta}{2} < 1 - \frac{\sqrt{\beta^2 - 4\gamma}}{2}, \\ -1 + \frac{\sqrt{\beta^2 - 4\gamma}}{2} < \frac{\beta}{2} < 1 + \frac{\sqrt{\beta^2 - 4\gamma}}{2}. \end{cases}$$

Now we can mix these together,

$$\begin{cases} -\left(1 + \frac{\sqrt{\beta^2 - 4\gamma}}{2}\right) < \frac{\beta}{2} < 1 + \frac{\sqrt{\beta^2 - 4\gamma}}{2}, \\ -\left(1 - \frac{\sqrt{\beta^2 - 4\gamma}}{2}\right) < \frac{\beta}{2} < 1 - \frac{\sqrt{\beta^2 - 4\gamma}}{2}. \end{cases}$$

so as to put it into the following more compact form:

$$\frac{|\beta|}{2} < 1 - \frac{\sqrt{\beta^2 - 4\gamma}}{2}.$$

It follows that

$$1 - \frac{|\beta|}{2} > \frac{\sqrt{\beta^2 - 4\gamma}}{2}, \tag{2.6}$$

and since $\sqrt{\beta^2 - 4\gamma} \geq 0$, we get

$$\frac{|\beta|}{2} < 1. \tag{2.7}$$

In addition, we can square both sides of (2.6), since they are both positive, and obtain

$$\begin{aligned} 1 + \frac{\beta^2}{4} - |\beta| &> \frac{\beta^2}{4} - \gamma \\ \Rightarrow 1 - |\beta| &> -\gamma \\ \Rightarrow |\beta| &< 1 + \gamma, \end{aligned} \tag{2.8}$$

which is one of the Jury conditions. To obtain the other Jury condition, note that since $\beta^2 \geq 4\gamma$, we can write

$$\left(\frac{|\beta|}{2}\right)^2 \geq \gamma. \tag{2.9}$$

Combining (2.7) and (2.9) gives $\gamma \leq \left(\frac{|\beta|}{2}\right)^2 < 1^2 = 1$, and hence $\gamma + 1 < 2$, which is the second Jury condition. The two Jury conditions together give

$$|\beta| < 1 + \gamma < 2,$$

which is what we were trying to prove.

Now putting together the results from “ \Rightarrow ” and “ \Leftarrow ”, we have shown (2.4):

$$|\beta| < 1 + \gamma < 2 \iff |\lambda| < 1.$$

Exercise 2.4.16: Romeo and Juliet in love/hate-preserving mode

(a)

$$\begin{aligned} \det A &= \det \begin{bmatrix} a_R - 1 & p_R \\ p_J & a_J - 1 \end{bmatrix} \\ &= (a_R - 1)(a_J - 1) - p_R p_J \\ &= (-p_J)(-p_R) - p_R p_J \\ &= 0, \text{ as required} \end{aligned}$$

(b)

$$J = \begin{bmatrix} a_R & p_R \\ p_J & a_J \end{bmatrix}$$

The eigenvalues are given by

$$\begin{aligned} \det \begin{bmatrix} a_R - \lambda & p_R \\ p_J & a_J - \lambda \end{bmatrix} &= (\lambda - a_R)(\lambda - a_J) - p_R p_J \\ &= \lambda^2 - (a_R + a_J)\lambda + a_R a_J - p_R p_J \\ &= \lambda^2 - (a_R + a_J)\lambda + a_R + a_J - 1 \quad (\text{since } \det A = (a_R - 1)(a_J - 1) - p_R p_J = 0) \\ &= [\lambda - 1][\lambda - (a_R + a_J - 1)] = 0, \end{aligned}$$

That is, $\lambda = 1$ or $\lambda = a_R + a_J - 1$, as required.

Exercise 2.4.17: Host-parasitoid systems: the Poisson distribution

$$\begin{aligned} \sum_{i=0}^{\infty} P(i) &= \sum_{i=0}^{\infty} \frac{\nu^i e^{-\nu}}{i!} \\ &= e^{-\nu} \sum_{i=0}^{\infty} \frac{\nu^i}{i!} \\ &= e^{-\nu} e^{\nu} \quad (\text{Taylor expansion}) \\ &= 1 \end{aligned}$$

Exercise 2.4.18: Host-parasitoid systems: the Nicholson-Bailey model

(a) Fixed points (H, P) must satisfy

$$\begin{aligned} H &= kHe^{-aP} \\ P &= cH[1 - e^{-aP}] \end{aligned}$$

The first equation gives $H = 0$ or $P = \frac{\ln k}{a}$.

Substituting $H = 0$ into the second equation gives $P = 0$, thus yielding the trivial fixed point,

$$(H_1^*, P_1^*) = (0, 0).$$

Substituting $P = \frac{\ln k}{a}$ into the second equation gives $H = \frac{k \ln k}{ac(k-1)}$, yielding the nontrivial fixed point,

$$(H_2^*, P_2^*) = \left(\frac{k \ln k}{ac(k-1)}, \frac{\ln k}{a} \right).$$

To ensure $P_2^* > 0$, we require $k > 1$.

(b)

$$J(H, P) = \begin{bmatrix} ke^{-aP} & -akHe^{-aP} \\ c[1 - e^{-aP}] & acHe^{-aP} \end{bmatrix},$$

so

$$J(H_1^*, P_1^*) = J(0, 0) = \begin{bmatrix} k & 0 \\ 0 & 0 \end{bmatrix}.$$

The eigenvalues are $\lambda_1 = k$ and $\lambda_2 = 0$. Thus, the trivial fixed point is stable when $0 < k < 1$, and unstable when $k > 1$.

(c)

$$\begin{aligned} \ln k + \frac{\ln k}{k-1} &> 1 \\ \iff \ln k \left(\frac{k}{k-1} \right) &> 1 \\ \iff k \ln k &> k-1 \\ \iff k \ln k - k + 1 &> 0. \end{aligned}$$

Let $f(k) = k \ln k - k + 1$. Since $f'(k) = 1 + \ln k - 1 = \ln k > 0$, we see that $f(k)$ is a monotonically increasing function for $k > 1$. Further, $f(1) = 0$.

thus

$$k \ln k - k + 1 > 0,$$

or

$$\ln k + \frac{\ln k}{k-1} > 1,$$

as required.

Exercise 2.4.19: Host-parasitoid systems: the Beddington model

Note that the problem as stated in the text is very challenging. As such, this solution is not complete, but reflects approximately what we would expect a student to be able to do.

(a) We can find two trivial fixed points by inspection, namely

$$(\bar{H}_1, \bar{P}_1) = (0, 0)$$

and

$$(\bar{H}_2, \bar{P}_2) = (K, 0).$$

The first of these fixed points represents the situation that both hosts and parasitoids are extinct. The second represents the situation that the parasitoids are extinct, and the host population is at its carrying capacity.

There is a third fixed point, representing co-existence. This fixed point cannot be solved for explicitly (our apologies for the misleading wording in the problem statement). Please consult the paper by Beddington, Free and Lawton for details on how they handled this case (see text for the complete reference to the paper).

(b) We can determine the stability of the two trivial fixed points found above.

The Jacobian matrix of the Beddington model is

$$J(\bar{H}, \bar{P}) = \begin{pmatrix} \exp \left[r \left(1 - \frac{\bar{H}}{K} \right) - a\bar{P} \right] \left(1 - \frac{\bar{H}r}{K} \right) & -a\bar{H} \exp \left[r \left(1 - \frac{\bar{H}}{K} \right) - a\bar{P} \right] \\ c(1 - e^{-a\bar{P}}) & ac\bar{H}e^{-a\bar{P}} \end{pmatrix}.$$

The stability of $(\bar{H}_1, \bar{P}_1) = (0, 0)$ is determined by

$$J(0, 0) = \begin{pmatrix} e^r & 0 \\ 0 & 0 \end{pmatrix}.$$

Here, $\text{tr } J = e^r$ and $\det J = 0$. Since $r > 0$ (why?), $\text{tr } J > 1$, and hence the fixed point $(\bar{H}_1, \bar{P}_1) = (0, 0)$ is unstable.

The stability of $(\bar{H}_2, \bar{P}_2) = (K, 0)$ is determined by

$$J(K, 0) = \begin{pmatrix} 1 - r & -aK \\ 0 & acK \end{pmatrix}.$$

Here, $\text{tr } J = 1 - r + acK$ and $\det J = acK(1 - r)$. Depending on the value of the model parameters, this fixed point may be stable or unstable. Stability is guaranteed by the Jury conditions, which are

$$|1 - r + acK| < 1 + acK(1 - r) < 2.$$

Determining the conditions that guarantee stability of the steady state representing co-existence is beyond the scope of this book and solution manual. The reader is encouraged to consult the paper by Beddington, Free and Lawton for details. It turns out that the co-existence fixed point is stable in a large region of parameter space, especially for small values of r . For large values of r , the fixed point usually is unstable (depending on the values of the other model parameters).

- (c) The numerical experiment is left to the reader. Lots of interesting patterns are possible depending on the choice of parameters. It is especially revealing to plot the orbits in the (H, P) phase plane. We refer the reader to the book *Mathematical Models in Biology* by Leah Edelstein-Keshet for a nice discussion of a variety of numerical solutions.

3.9 Exercises for ODEs

Exercise 3.9.1: The C^{14} -method

Let $C(t)$ be the concentration of carbon at any time t . We use the equation described in the chapter on ODEs,

$$C'(t) = -k C(t),$$

where $k > 0$ is a constant. This equation has the solution

$$C(t) = Ae^{-kt},$$

where A is a constant of integration. From the initial condition, $C(0) = c_0$, we find that $A = c_0$, so the equation we get for C is

$$C(t) = c_0 e^{-kt}.$$

We know by definition that $C(T_{1/2}) = \frac{1}{2}c_0 = c_0 e^{-kT_{1/2}}$. Solving for k , we find

$$k = \frac{\log(2)}{T_{1/2}}.$$

The wood now has 75% of its original concentration. Call the time $T_{3/4}$. Currently, we have $C(T_{3/4}) = \frac{3}{4}c_0$. We set this value for the function and solve for $T_{3/4}$:

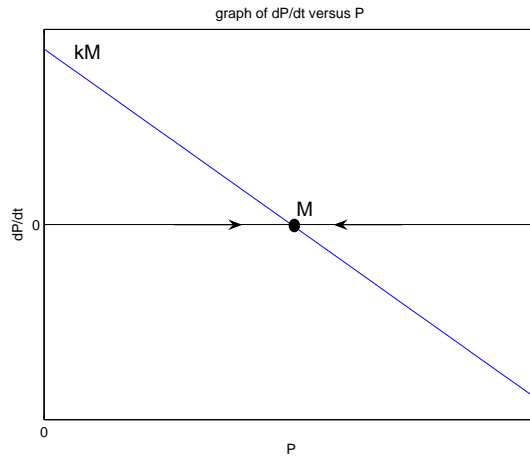
$$\begin{aligned} \frac{3}{4}c_0 &= c_0 e^{-kT_{3/4}} \\ \Rightarrow \log(4/3) &= kT_{3/4} \\ \Rightarrow T_{3/4} &= \log(4/3) \cdot \frac{1}{k} \\ &= T_{1/2} \cdot \frac{\log(4/3)}{\log(2)} \\ &= 2390 \text{ a} \end{aligned}$$

The model tells us that this piece of wood is about 2390 years old. This is about 1000 years after Tutankhamen's time (about 3300 years ago), so Tutankhamen could *not* have sat in a boat made of wood from the same tree that this piece came from.

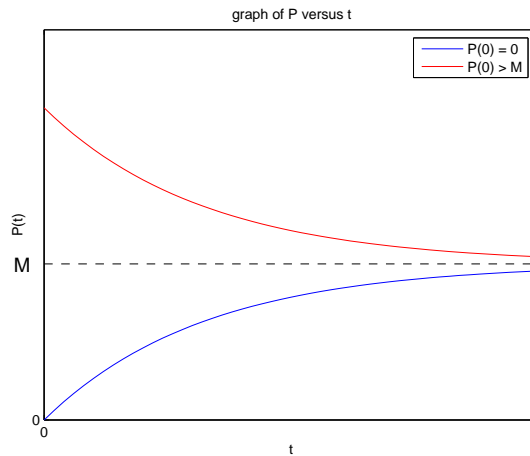
Exercise 3.9.2: Learning curves

- dP/dt represents the rate of change of the performance over time, or how fast someone picks up a skill.
- When $M \geq P$, $dP/dt \geq 0$, so $P(t)$ is increasing or staying constant in time. If $M < P$, then $dP/dt < 0$, which means that $P(t)$ is decreasing in time. We expect that with more and more training, a person will never have a

decrease in performance. Notice that if a we start with P below M , P can never get larger than M . If $P = M$, P will remain constant. This model is reasonable. We interpret M as the level when someone has mastered the skill (M for master). A reasonable initial condition could be $P(0) = 0$; no previous knowledge.



(c)



Exercise 3.9.3: Harvesting

The differential equation we have is

$$u'(t) = g(u),$$

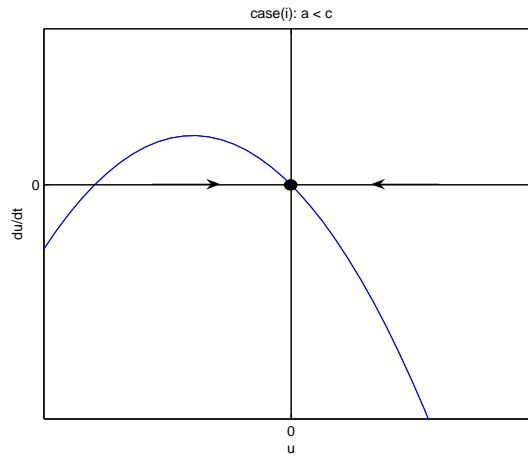
where $g(u) = au(1 - u/K) - cu$. Rewriting, we get

$$g(u) = u \left((a - c) - \frac{a}{K}u \right).$$

We can see that the graph of $g(u)$ vs u is a parabola. Since $a, K > 0$, the parabola opens downwards. It has intersections with the u axis at $u = 0$ and at $u = \frac{K}{a}(a - c)$. We refer to $u = 0$ as the trivial steady state, and $u = \frac{K}{a}(a - c)$ as the nontrivial steady state.

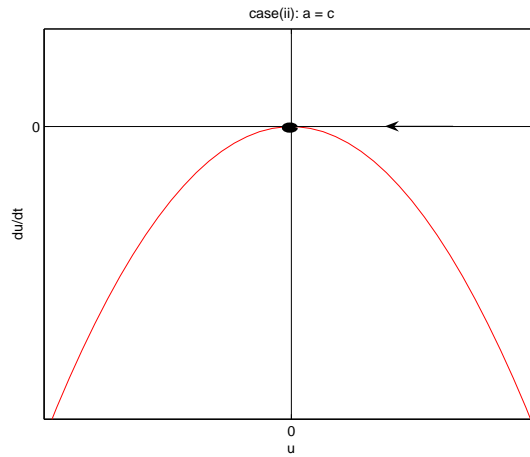
There are 3 different scenarios which will give three different qualitative sketches.

- Case (i): $a < c$. This means that the nontrivial steady state is negative. There is only one biologically realistic steady state, namely the trivial steady state $u = 0$.



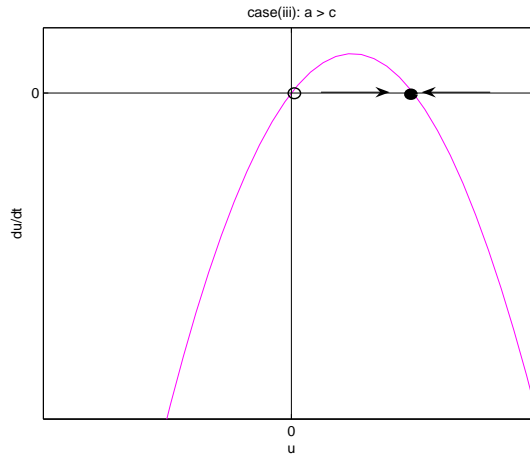
The phase portrait shows that the trivial steady state $u = 0$ is stable.

- Case (ii): $a = c$. Now there is just one intersection, at the origin. Hence there is only one steady state, namely the trivial steady state $u = 0$.



The phase portrait shows that $u = 0$ is stable (for $u > 0$).

- Case (iii): $a > c$. Both steady states are biologically realistic.



The phase portrait shows that the nontrivial steady state at $u = \frac{K}{a}(a - c)$ is stable, and the trivial one at $u = 0$ is unstable.

In summary, the nontrivial steady state exists only for $a > c$, and it is stable. If $a \leq c$, there is only the trivial steady state, and it is stable.

Biologically, this means that when the population is not reproducing faster than it is being harvested, it will die out. If it is reproducing fast enough, it settles down

to a steady state, determined by how much faster it is reproducing than it is being harvested (the larger the difference, the larger the population at the steady state).

Exercise 3.9.4: Fishing

- (a)
- 1: The fishing term says that there is a constant number of fish per unit time being removed due to fishing. This number is H_1 , in the units of fish per unit time.
 - 2: Here the fishing term says that the number of fish which are fished out per unit time is proportional to the current population. H_2 , which is the fraction of fish caught per unit time, must be between 0 and 1, since you cannot catch more than all of the fish, or fewer than none of them. This model reflects the fact that fish must be found to be caught. A certain fraction of them can be found.
 - 3: In the third model, the limits of small and large values for N reduce to models 2 and 1, respectively. As $N \rightarrow 0$, the fishing term, $H_3N/(A + N)$, goes to H_3N/A . This is the same situation as model 2, but with H_2 “=” H_3/A . That is, for small amounts of fish, the number of fish caught per unit time is proportional to the population. More fish implies more fishing, and fewer fish implies less fishing. As $N \rightarrow \infty$, the fishing term will go to H_3 , a constant, which works the same way as H_1 in model 1. That is, when there are more fish than can be caught, or more fish than are wanted, there is just a constant amount of fish being caught per unit time. A determines how fast this limit of “too many” fish is effectively reached. When A is higher, model 3 stays at model 2 for a longer time. When A is lower, model 3 turns into model 1 sooner. We can see that A is actually in the units of fish. When $N = A$, we see that the fishing term becomes $H_3/2$, giving an idea of how fast we are approaching the limit of H_3 , in terms of N .
- (b) Model 1 is not biologically realistic because a constant number of fish caught per unit time regardless of how many fish there are makes no sense. For example, suppose there are 10 fish in the pond, and $H_1 = 3$ fish/hour. Neglecting the first term in the model equation, there is no way that this model can work after 3 hours, because there will be only 1 fish left. Model 1 would work only if there was an abundance of fish. When the abundance becomes less, and the fish population becomes closer to the value H_1 , the model breaks down.
- (c) Model 3 is a better model, because, as explained in part (a), it takes the best parts of both models. We see that model 3 is precisely the modification to model 1 desired in part (b). The problem with model 2 is that there is a limited number of fish which can actually be caught. Model 3 says what happens when this limit is reached. For example, say you have a boat which can catch 50 fish per hour. We use model 2. Say that $H_2 = 0.5$, and that initially, $N = 100$. After an hour, you will have caught 50 fish. After 2 hours,

you will have caught 25 more fish, etc. If, on the other hand, you start fishing at $N = 1000$, then model 2 says you will have caught 500 fish after an hour, even though your boat can catch only 50 fish per hour. Model 3 corrects this and says that there is a constant number of fish that will be caught, when the population is high. To a close approximation, H_3 represents the combined effects of people who fish with limited boat capacities, or limited desired quantities of fish, and puts it into a single term; one big “boat” which can catch at the most $\|H_3\|$ fish per hour, where $\|H_3\|$ means the magnitude of H_3 , without the units.

Exercise 3.9.5: A metapopulation model

Thanks to Pandora Lam, University of Alberta, for providing this solution.

- (a) We first rewrite P' :

$$\begin{aligned} P' &= cP(h - P) - \mu P \\ &= chP - cP^2 - \mu P \\ &= (ch - \mu)P - cP^2 \\ &= P((ch - \mu) - cP) \end{aligned}$$

and then set $P' = 0$ to find the steady states, namely $P = 0$ and $P = \frac{ch - \mu}{c} = h - \frac{\mu}{c}$.

Note that the steady state $P = 0$ always exists. The steady state $P = h - \frac{\mu}{c}$ exists only if $h - \frac{\mu}{c} > 0$ or $h > \frac{\mu}{c}$.

- (b) Let $f(P) = cP(h - P) - \mu P$. Then $f'(P) = ch - \mu - 2cP$.

The stability of the steady state $P = 0$ is determined by $f'(0) = ch - \mu$.

If $h > \frac{\mu}{c}$, $f'(0) > 0$, and $P = 0$ is a stable steady state.

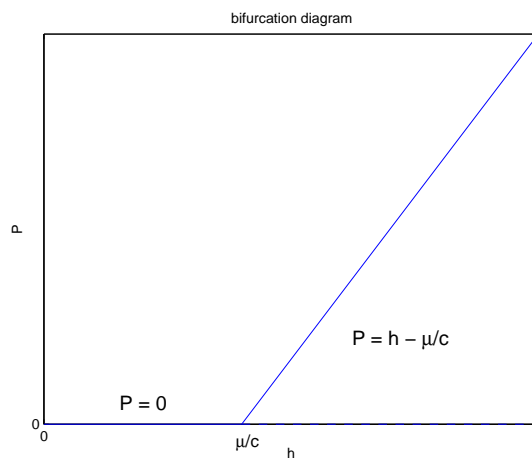
If $h < \frac{\mu}{c}$, $f'(0) < 0$, and $P = 0$ is an unstable steady state.

The stability of the steady state $P = h - \frac{\mu}{c}$ is determined by

$$f'(h - \frac{\mu}{c}) = ch - \mu - 2c(h - \frac{\mu}{c}) = -(ch - \mu).$$

Recall that this steady state exists only if $h > \frac{\mu}{c}$, so that $f'(h - \frac{\mu}{c}) < 0$, which implies that the steady state is stable.

The bifurcation diagram follows:



In conclusion, the population dies out as soon as the number of habitable patches falls below $\frac{\mu}{c}$.

Note that the horizontal line in the bifurcation diagram should be dotted for $h > \mu/c$.

Exercise 3.9.6: Gene activation

- (a) The first term is a constant growth term. The growth of g depends linearly on the concentration of S , with a growth rate k_1 . In this case, it is a constant growth, because s_0 is constant.

The second term is the gene's natural decay term. With nothing else, the gene would decay exponentially at a rate k_2 .

The third term is a self-production term, with a limited rate of reproduction of k_3 . When g gets large, this term becomes approximately constant, keeping at the k_3 factor ($\lim_{g \rightarrow \infty} \frac{g^2}{k_4^2 + g^2} = 1$). The parameter k_4 determines how large g has to be before this term starts behaving as in the large g limit.

- (b) We start with the first equation,

$$\frac{dg}{dt} = k_1 s_0 - k_2 g + \frac{k_3 g^2}{k_4^2 + g^2}.$$

In order to get the last term to look like $x^2/(1+x^2)$, we must divide everything by k_3 , and then cleverly multiply the last term by 1, as in $\frac{1/k_4^2}{1/k_4^2} = 1$. We then get:

$$\frac{1}{k_3} \frac{dg}{dt} = \frac{k_1 s_0}{k_3} - \frac{k_2}{k_3} g + \frac{(g/k_4)^2}{1 + (g/k_4)^2}$$

It seems logical to define $x := g/k_4$, so that the last term is correct. We now must think about how we can define τ in order to make the $dx/d\tau = \frac{1}{k_3} dg/dt$. To get just a single $\frac{1}{k_3}$ as the difference, we'll need $\tau = \frac{k_3}{k_4} t$, to cancel out the k_4 's and to bring in the $\frac{1}{k_3}$. Since x and τ are just scalar multiples of g and t , respectively, we can pull the scalars out of the differential operator, so that

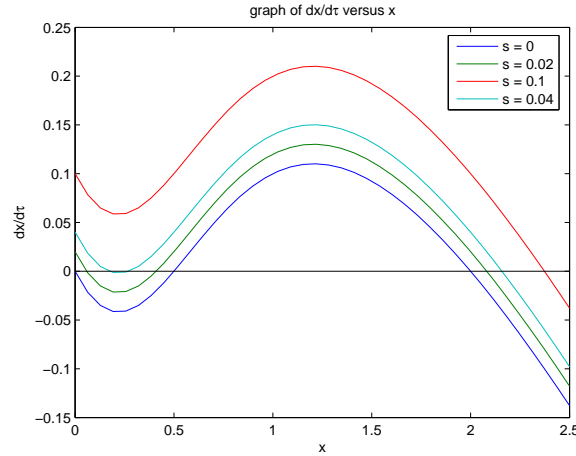
$$\frac{dx}{d\tau} = \frac{d(g/k_4)}{d(k_3 t/k_4)} = \frac{1/k_4}{k_3/k_4} \frac{dg}{dt} = \frac{1}{k_3} \frac{dg}{dt}.$$

Hence,

$$\begin{aligned} \frac{dx}{d\tau} &= \frac{1}{k_3} \frac{dg}{dt} \\ &= \frac{k_1 s_0}{k_3} - \frac{k_2}{k_3} g + \frac{(g/k_4)^2}{1 + (g/k_4)^2} \\ &= \frac{k_1 s_0}{k_3} - \frac{k_2 k_4}{k_3} x + \frac{x^2}{1 + x^2} \\ &= s - rx + \frac{x^2}{1 + x^2}, \end{aligned}$$

with $s := k_1 s_0/k_3$, and $r := k_2 k_4/k_3$.

- (c) We really need to graph only two more cases; when s is such that there are two intersections of the horizontal axis, and when s is high enough that there are no intersections of the horizontal axis.



- (d) We note that a bifurcation in the number of steady states occurs at $s^* \approx 0.04$. For $s < s^*$, there are three steady states; the outer two steady states are stable, and the inner steady state is unstable. For $s > s^*$, there is one stable steady state. The bifurcation diagram follows: