MATH3070 Assignment 2

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Question 1

We have the predator-prey population model given by

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{k}\right) - v(N)P$$
$$\frac{dP}{dt} = cv(N)P - mP - qEP$$

where

$$v(N) = \frac{aN}{1 + ahN}$$

is the rate of prey consumption per predator.

(a) If we have the equation

$$V = a(T - Vh)N$$

that models the number of prey getting eaten per predator in some duration of time, we can see that the term $T - Vh$ in the equation says how much 'free' time the predators would have in the time interval $[0, T]$ after catching and eating V prey. This is because h is the handling time, and so Vh is the time needed for a predator to eat V prey. Since there is a total of T time, the entire term models how much time a predator has after catching and eating V prey.

(b) Now, we derive the rate of prey consumption $v(N)$ per predator from the equation $V(N)$ given. First, expand

$$\begin{aligned} V &= a(T - Vh)N \\ &= aTN - aVhN \\ \Rightarrow V(1 + ahN) &= aTN \\ V &= \frac{aTN}{1 + ahN} \end{aligned}$$

Since we want the *rate* of prey being eaten, we take the time derivative, yielding

$$\begin{aligned} v(N) = \frac{dV}{dT} &= \frac{d}{dT}\left(\frac{aTN}{1 + ahN}\right) \\ &= \frac{aN}{1 + ahN} \end{aligned}$$

assuming that a, N, and h are effectively constant in time. This is exactly the equation for the rate of prey consumption given, derived from $V(N)$.

(c) Now we aim to non-dimensionalise the two models. Start by defining $N = n_0 x$ and $P = p_0 y$. Note that $[x] = [y] = 1$, and $[n_0] =$ unit prey while $[p_0] =$ unit predator.
Also, to ensure consistency in units, we write $v(N)$ as

$$v(N) = b\left(\frac{aN}{1 + ahN}\right)$$

where $b = 1$ and $[b] = 1/(\text{unit predator})$. Hence $[v(N)] = (\text{unit prey}) \ / \ (\text{unit predator} \cdot \text{time})$, and consequently

$$\left[\frac{aN}{1 + ahN}\right] = \frac{\text{unit prey}}{\text{time}}$$

Now we note that $[a] = 1/\text{time}$ and $[N] = \text{unit prey}$, so the term $1 + ahN$ must be unitless. Therefore we obtain the expected unit for h as $[h] = \text{time} / (\text{unit prey})$.
Finally, we define $t = t_0\tau$, where $[t_0] = [t] = \text{time}$, with τ unitless. Making these substitutions so far, we obtain

$$\begin{aligned}\frac{dN}{dt} &= \frac{n_0}{t_0}\frac{dx}{d\tau} = rn_0x\left(1 - \frac{n_0}{k}x\right) - bp_0y\left(\frac{an_0x}{1+ahn_0x}\right)\\ \Rightarrow \frac{dx}{d\tau} &= rt_ox\left(1 - \frac{n_0}{k}x\right) - abp_0t_0y\left(\frac{x}{1+ahn_0x}\right)\end{aligned}$$

We can choose $t_0 = 1/r$ and $\gamma = k/n_0$ to remove some constants here. As a check, we have that $[r] = 1/\text{time} \Rightarrow [t_0] = \text{time}$ as needed. Further, we have $[k] = [n_0] = \text{unit prey} \Rightarrow [\gamma] = 1$ as needed.
At the same time, we can choose $n_0 = 1/ah$ to remove the constants in one of the denominators. To check unit consistency, we have

$$[n_0] = \text{unit prey} = \left(\frac{1}{\left(\frac{1}{\text{time}}\right)\left(\frac{\text{time}}{\text{unit prey}}\right)}\right) = \left[\frac{1}{ah}\right]$$

as needed. Similarly, define $p_0 = 1/abt_0$. To check unit consistency, we have

$$[p_0] = \text{unit predator} = \left(\frac{1}{\left(\frac{1}{\text{time}}\right)\left(\frac{1}{\text{unit predator}}\right)(\text{time})}\right) = \left[\frac{1}{abt_0}\right]$$

as needed. Substituting in all of these defined variables and simplifying, we obtain

$$\frac{dx}{d\tau} = x\left(1 - \frac{x}{\gamma} - \frac{y}{1+x}\right)$$

which is the non-dimensionalised form of the prey differential model. Now we turn to the predator population model, making the initial substitution:

$$\begin{aligned}\frac{dP}{dt} &= \frac{p_0}{t_0}\frac{dy}{d\tau} = cb\left(\frac{an_0x}{1+ahn_0x}\right)p_0y - mp_0y - qEp_0y\\ \Rightarrow \frac{dy}{d\tau} &= bct_0\left(\frac{an_0x}{1+x}\right)y - t_0my - t_0qEy\end{aligned}$$

We can define $\beta = abct_0n_0$ and check the units:

$$[\beta] = [abct_0n_0] = \left(\text{time} \cdot \text{unit prey} \cdot \frac{1}{\text{time}} \cdot \frac{1}{\text{unit predator}} \cdot \frac{\text{unit predator}}{\text{unit prey}}\right) = 1$$

which is unitless as desired. Hence,

$$\frac{dy}{d\tau} = \beta y\left(\frac{x}{1+x} - t_0\left[\frac{m+qE}{\beta}\right]\right)$$

Now we define

$$\alpha = t_0\left[\frac{m+qE}{\beta}\right] \quad \Rightarrow \quad [\alpha] = \text{time}\left(\frac{1/\text{time} + 1/(\text{time} \cdot \text{effort}) \cdot \text{effort}}{1}\right) = 1$$

And with this, we have the non-dimensionalised system as

$$\begin{aligned}\frac{dx}{d\tau} &= x\left(1 - \frac{x}{\gamma} - \frac{y}{1+x}\right)\\ \frac{dy}{d\tau} &= \beta y\left(\frac{x}{1+x} - \alpha\right)\end{aligned}$$

(d) Now our goal is to find equilibria, and the conditions for when those equilibria are biologically meaningful. To find an equilibrium for a system of DEs, we need values of the parameters such that *both* of the DEs are equal to 0, i.e. $dx/d\tau = 0 = dy/d\tau$:

$$x\left(1 - \frac{x}{\gamma} - \frac{y}{1+x}\right) = 0 = \beta y\left(\frac{x}{1+x} - \alpha\right)$$

We can immediately see that $(x^*, y^*) = (0, 0)$ is a solution (equilibrium) here. Now, we can check for more by looking at each DE at a time, starting with $dx/d\tau$:

$$
\begin{aligned}
0 = x\left(1 - \frac{x}{\gamma} - \frac{y}{1+x}\right) &\Rightarrow 0 = 1 - \frac{x}{\gamma} - \frac{y}{1+x} \\
\Rightarrow y = (1+x)\left(1 - \frac{x}{\gamma}\right)
\end{aligned}
$$

We can substitute this into our DE for y, giving

$$
\begin{aligned}
0 &= \beta y\left(\frac{x}{1+x} - \alpha\right) \\
&= \beta x\left(1 - \frac{x}{\gamma}\right) - \alpha\beta(1+x)\left(1 - \frac{x}{\gamma}\right)
\end{aligned}
$$

which, for strictly positive x, we only have a solution for $x/\gamma = 1$, and so we have an equilibrium solution for $x^* = \gamma$. We can now backsubstitute this in to our formula for the equilibrium y value, giving

$$
y^* = (1+\gamma)(1-1) = 0
$$

and so we have a second solution (equilibrium) at $(x^*, y^*) = (\gamma, 0)$.
Finally, we check for one more solution, this time by manipulating $dy/d\tau = 0$:

$$
\begin{aligned}
0 &= \beta y\left(\frac{x}{1+x} - \alpha\right) \\
\Rightarrow \frac{x}{1+x} &= \alpha \\
\alpha &= x - \alpha x = x(1-\alpha) \\
\Rightarrow x^* &= \frac{\alpha}{1-\alpha}
\end{aligned}
$$

which will be our equilibrium x value. We can substitute this into $dx/d\tau$ now to find the equilibrium y value:

$$
\begin{aligned}
0 &= x\left(1 - \frac{x}{\gamma} - \frac{y}{1+x}\right) \\
&= 1 - \frac{x}{\gamma} - \frac{y}{1+x} \\
\Rightarrow y &= (1+x)\left(1 - \frac{x}{\gamma}\right) \\
&= \left(1 + \frac{\alpha}{1-\alpha}\right)\left(1 - \frac{\alpha}{(1-\alpha)\gamma}\right) \\
&= \frac{1}{1-\alpha}\left(\frac{\gamma(1-\alpha) - \alpha}{(1-\alpha)\gamma}\right) \\
\Rightarrow y^* &= \frac{\gamma - \frac{\alpha}{1-\alpha}}{(1-\alpha)\gamma}
\end{aligned}
$$

and so our final equilibrium is at $(x^*, y^*) = \left(\frac{\alpha}{1-\alpha}, \frac{\gamma - \frac{\alpha}{1-\alpha}}{(1-\alpha)\gamma}\right)$.
Now, we note that the mutual extinction equilibrium is biologically meaningful by default (since it doesn't rely on any parameters, and has both populations set to 0). The second, predator-extinction equilibrium at $(x^*, y^*) = (\gamma, 0)$ is meaningful for $\gamma > 0$ (the case where $\gamma = 0$ would reduce to mutual extinction). The final case, $(x^*, y^*) = \left(\frac{\alpha}{1-\alpha}, \frac{\gamma - \frac{\alpha}{1-\alpha}}{(1-\alpha)\gamma}\right)$, for presumably coexistent populations is meaningful for $0 < \alpha < 1$ ($\alpha = 0$ reduces to extinction, and $\alpha = 1$ involves dividing by zero), along with $\gamma > 0$ as before, with the additional constraint that

$$
\gamma - \frac{\alpha}{1-\alpha} > 0 \quad \Longrightarrow \quad \gamma > \frac{\alpha}{1-\alpha}
$$

With these conditions, we have biologically meaningful equilibria.

(e) The stability conditions for the mutual extinction equilibrium can be found by assessing the eigenvectors of the Jacobian matrix evaluated at the equilibrium. We calculate the Jacobian as

$$\begin{aligned}
\mathcal{J} &= \left.\begin{pmatrix} \frac{\partial f_1}{\partial x} & \frac{\partial f_1}{\partial y} \\ \frac{\partial f_2}{\partial x} & \frac{\partial f_2}{\partial y} \end{pmatrix}\right|_{(x^*,y^*)=(0,0)} \\
&= \left.\begin{pmatrix} \frac{\partial \dot{x}}{\partial x} & \frac{\partial \dot{x}}{\partial y} \\ \frac{\partial \dot{y}}{\partial x} & \frac{\partial \dot{y}}{\partial y} \end{pmatrix}\right|_{(x^*,y^*)=(0,0)} \\
&= \left.\begin{pmatrix} 1 - \frac{2x}{\gamma} - \frac{y}{(x+1)^2} & -\frac{x}{1+x} \\ \frac{\beta y}{(1+x)^2} & \beta\left(\frac{x}{1+x} - \alpha\right) \end{pmatrix}\right|_{(x^*,y^*)=(0,0)} \\
&= \begin{pmatrix} 1 & 0 \\ 0 & -\alpha\beta \end{pmatrix}
\end{aligned}$$

The eigenvalues are then found by

$$\begin{aligned}
0 = \det(\mathcal{J} - \lambda I) = \det \begin{pmatrix} 1-\lambda & 0 \\ 0 & -\alpha\beta - \lambda \end{pmatrix} \\
= (1-\lambda)(-\alpha\beta - \lambda)
\end{aligned}$$

which has eigenvalues $\lambda_{1,2} = 1, -\alpha\beta$. We know that β is positive by construction (of all positive constants). Similarly, the physical significance of α only makes sense for $\alpha \geq 0$ (given that α is related to the mortality and harvesting of the predator species), and so $-\alpha\beta \leq 0$. Therefore, we have one positive and one negative eigenvalue, and so the mutual extinction equilibrium is a saddle (i.e. unstable).

(f) We now assess the stability of the predator-extinction equilibrium by the same process:

$$\begin{aligned}
\mathcal{J} &= \left.\begin{pmatrix} 1 - \frac{2x}{\gamma} - \frac{y}{(x+1)^2} & -\frac{x}{1+x} \\ \frac{\beta y}{(1+x)^2} & \beta\left(\frac{x}{1+x} - \alpha\right) \end{pmatrix}\right|_{(x^*,y^*)=(\gamma,0)} \\
&= \begin{pmatrix} 1 & -\frac{\gamma}{1+\gamma} \\ 0 & \beta\left(\frac{\gamma}{1+\gamma} - \alpha\right) \end{pmatrix}
\end{aligned}$$

As before, set

$$0 = \det(\mathcal{J} - \lambda I) = (-1-\lambda)\left(\beta\left[\frac{\gamma}{1+\gamma} - \alpha\right] - \lambda\right) - 0$$

Therefore we have the eigenvalues $\lambda_{1,2} = -1, \beta(\gamma/(1+\gamma) - \alpha)$. We know $\gamma > 0$ for meaningful equilibria, and so $0 < \gamma/(1+\gamma) < 1$. Similarly, we also need $0 < \alpha < 1$. Therefore, if $\alpha > \gamma/(1+\gamma)$, we have a stable sink node since both eigenvalues will be real and negative. Otherwise, we will have one positive and one negative real eigenvalue resulting in an unstable saddle.

(g) Finally, we want to show when the coexistence equilibrium is stable:

$$\mathcal{J} = \left.\begin{pmatrix} 1 - \frac{2x}{\gamma} - \frac{y}{(x+1)^2} & -\frac{x}{1+x} \\ \frac{\beta y}{(1+x)^2} & \beta\left(\frac{x}{1+x} - \alpha\right) \end{pmatrix}\right|_{(x^*,y^*)=\left(\frac{\alpha}{1-\alpha}, \frac{\gamma - \frac{\alpha}{1-\alpha}}{(1-\alpha)\gamma}\right)}$$

To find the eigenvalues, we set $\det(\mathcal{J} - \lambda I) = 0$:

$$
\begin{aligned}
0 &= \left(1 - \frac{2\alpha}{(1-\alpha)\gamma} - \frac{\gamma - \frac{\alpha}{1-\alpha}}{\gamma(1-\alpha)\left(1+\frac{\alpha}{1-\alpha}\right)^2} - \lambda\right)\left(\beta\left[\frac{\alpha}{(1-\alpha)\left(1+\frac{\alpha}{1-\alpha}\right)}\right] - \lambda\right) - \\
&\quad - \left(-\frac{\alpha}{(1-\alpha)\left(1+\frac{\alpha}{1-\alpha}\right)}\right)\left(\beta\frac{\gamma - \frac{\alpha}{1-\alpha}}{\gamma(1-\alpha)\left(1+\frac{\alpha}{1-\alpha}\right)^2}\right) \\
&= \left(\frac{(1-\alpha)\gamma - 2\alpha}{\gamma(1-\alpha)} - \frac{\gamma - \frac{\alpha}{1-\alpha}}{\gamma\left(1+\frac{\alpha}{1-\alpha}\right)} - \lambda\right)(\beta\left[\alpha - \alpha\right] - \lambda) - (-\alpha)\left(\beta\frac{\gamma - \frac{\alpha}{1-\alpha}}{\gamma\left(1+\frac{\alpha}{1-\alpha}\right)}\right) \\
&= \left(\frac{\gamma - 2\alpha\left(1+\frac{\alpha}{1-\alpha}\right) - \gamma + \gamma\alpha + \alpha}{\gamma} - \lambda\right)(-\lambda) + \alpha\beta\frac{\gamma - \gamma\alpha - \alpha}{\gamma} \\
&= \lambda^2 - \frac{\alpha}{\gamma}\left(\gamma - 1 - \frac{2\alpha}{1-\alpha}\right)\lambda + \alpha\beta\left(1 - \alpha - \frac{\alpha}{\gamma}\right)
\end{aligned}
$$

By the Routh Hurwitz criteria, a characteristic equation of the form $0 = \lambda^2 + A\lambda + B$ is stable (i.e. has negative real components of the eigenvalues) when both $A > 0$ and $B > 0$. So, for the coexistence equilibrium, we need

$$
\begin{aligned}
A &= -\frac{\alpha}{\gamma}\left(\gamma - 1 - \frac{2\alpha}{1-\alpha}\right) > 0 \\
B &= \alpha\beta\left(1 - \alpha - \frac{\alpha}{\gamma}\right) > 0
\end{aligned}
$$

For B, we have that β is strictly positive (as before) and $0 < \alpha < 1$. Hence we constrain positivity to $1 - \alpha - \alpha/\gamma > 0$, i.e.

$$1 > \alpha + \alpha/\gamma \quad \Rightarrow \quad \alpha < (1 + 1/\gamma)^{-1}$$

For A, we need $\gamma - 1 - 2\alpha/(1-\alpha) < 0$ for the whole term to be positive. i.e. $\gamma < 1 + 2\alpha/(1-\alpha)$, or $\gamma < (1+\alpha)/(1-\alpha)$. With all of these conditions, the coexistence equilibrium will be stable.

(h) We've plotted the three possible qualitative behaviours of the system of DEs in phase space, i.e. mutual extinction, predator extinction, and coexistence. This is shown in Figure 1. The python code to produce this diagram is attached in the assignment submission, and available at in the Github repository.

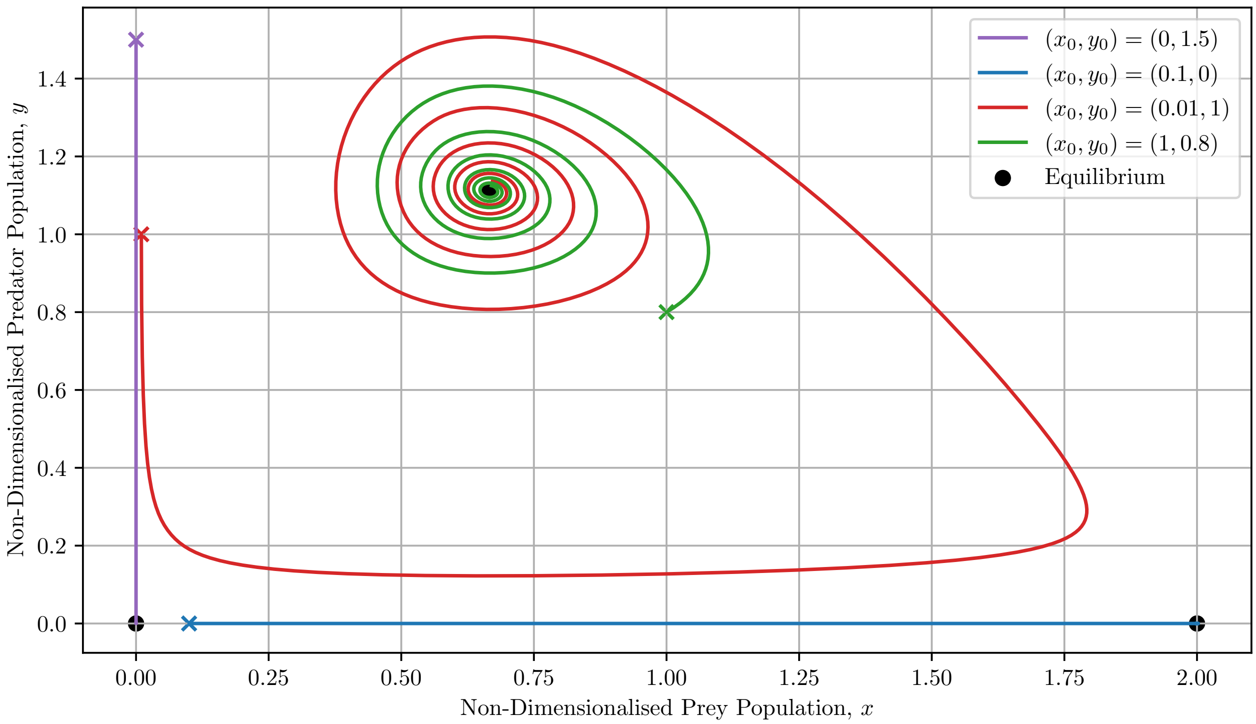

Figure 1: We see the behaviour of the system is greatly dependent on the initial conditions (x_0, y_0). The purple line shows mutual extinction, the blue shows predator extinction, and the red/green lines show coexistence from different initial conditions.

(i) The bifurcation diagram for the system of DEs, in terms of the non-dimensionalised parameters α and β is shown in Figure 2. As before, the code is available in the submission, or the in the Github repository.

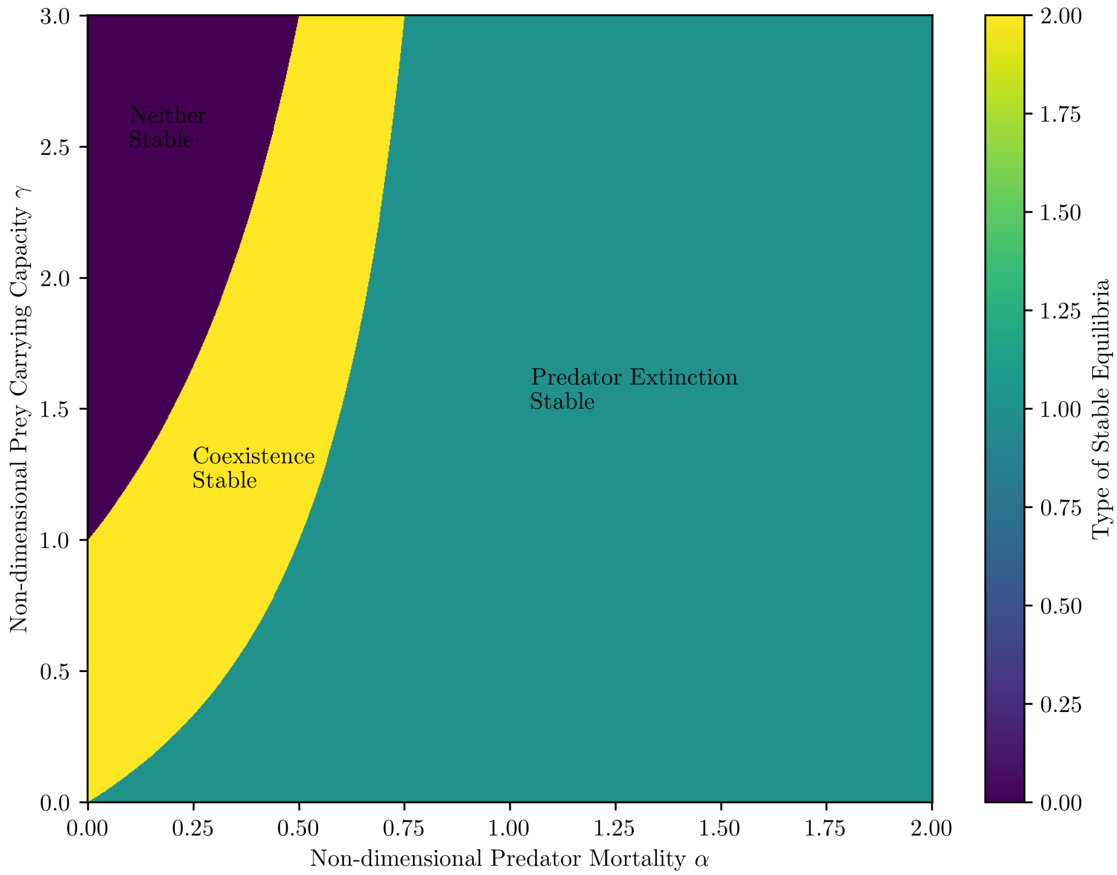

Figure 2: We plotted a 1000×1000 grid in parameter space and checked the criteria (defined in the previous question parts) for which stability case was satisfied. The purple region corresponds to a periodic orbit (which is not necessarily stable), while the yellow region represents stability (in either a node or spiral) for the coexistence equilibrium. The turquoise region is where the predator-extinction equilibrium is the only stable case.

(j) To aid in answering how the stability of the system changes as the fishing effort (i.e. α) is changed for a fixed γ, we created an animation of the behaviour of exactly that. Essentially, for a $\gamma > 0$, we expect the system stability to shift from periodic orbits to a stable spiral/node as α is increased. That is, for high enough fishing effort, we expect that the system should become more stable until such a point where the predator goes extinct. Since we can't be exactly sure of the true predator population, harvesting below this maximum threshold in α is the best idea to achieve maximum yield.

Question 2

We have a fish population that grows according to the model

$$x_{t+1} = \frac{ax_t}{b + x_t}$$

where we assume b is a known constant.

(a) We can evaluate the least squares estimate for the parameter a by taking the derivative of the sum of squared errors,

$$SSE(a) = \sum_{i=0}^{n-1} \left[x_{i+1} - \frac{ax_i}{b + x_i} \right]^2$$

with respect to a, and minimising (i.e. setting to zero):

$$\begin{aligned}
\frac{\partial SSE(a)}{\partial a} &= \frac{\partial}{\partial a}\left(\sum_{i=0}^{n-1} x_{i+1}^2 - \frac{2ax_ix_{i+1}}{b+x_i} + \frac{a^2x_i^2}{(b+x_i)^2}\right) = 0 \\
0 &= \sum_{i=0}^{n-1}\left(-\frac{2x_ix_{i+1}}{b+x_i} + \frac{2ax_i^2}{(b+x_i)^2}\right) \\
\Rightarrow \sum_{i=0}^{n-1}\frac{2x_ix_{i+1}}{b+x_i} &= \sum_{i=0}^{n-1}\frac{2ax_i^2}{(b+x_i)^2} \\
&= a\sum_{i=0}^{n-1}\frac{2x_i^2}{(b+x_i)^2} \\
\Rightarrow \hat{a} &= \frac{\sum_{i=0}^{n-1}\frac{x_ix_{i+1}}{b+x_i}}{\sum_{i=0}^{n-1}\frac{x_i^2}{(b+x_i)^2}}
\end{aligned}$$

Now with a formula for $\hat{a}$ found, we need to verify that it is a *least* squares estimate. We can check that this is the case with the double derivative test:

$$\begin{aligned}
\frac{\partial^2 SSE(a)}{\partial a^2} &= \frac{\partial}{\partial a}\frac{\partial SSE(a)}{\partial a} = \frac{\partial}{\partial a}\left[\sum_{i=0}^{n-1}\left(-\frac{2x_ix_{i+1}}{b+x_i} + \frac{2ax_i^2}{(b+x_i)^2}\right)\right] \\
&= \sum_{i=0}^{n-1}\frac{2x_i^2}{(b+x_i)^2}
\end{aligned}$$

and because of the squares in the numerator and denominator, this sum will always yield a positive result which means that $\hat{a}$ is in fact a least squares estimate.

(b) Using the python code attached (or available in the Github repo, we simulated data according to the aforementioned model with $b = 0.5$, $x_0 = 0.01$, $n = 20$, and $a = 1.5$. We found that $\hat{a} = 1.5 = a$ always (i.e. that it is an unbiased estimator) since the model is deterministic. As there is no random error on each time step, the simulated data always yields the model-predicted response exactly, and so the least squares estimate uses all of the available information to provide a perfect estimate.