Mathematical Biology Assignment 1

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Question

The growth rate of a fish species at time t is described by the equation

$$\frac{dg}{dt} = cg^{1/2}(t) - ag(t),$$

where c and a are positive constants. The initial condition is $g(0) = g_0$ (the initial size), where g_0 is a positive constant.

(a) Without solving the differential equation, determine $\lim_{t\to\infty} g(t)$.

SOLUTION:

To determine $\lim_{t\to\infty} g(t)$, we can find the stable steady state(s) of $g(t)$.

$$\frac{dg}{dt} = cg^{1/2}(t) - ag(t) \implies f(g) = cg^{1/2} - ag$$

Let g^* be a steady state, then we have $f(g^*) = 0 \iff c{g^*}^{1/2} - ag^* = 0$
Solving for g^* we have:

$${g^*}^{1/2}\left(c - a{g^*}^{1/2}\right) = 0$$

Which gives two roots:

$$\begin{aligned} {g_1^*}^{1/2} &= 0 & &\implies g_1^* = 0 \\ c - a{g_2^*}^{1/2} = 0 &\implies {g_2^*}^{1/2} = \frac{c}{a} & &\implies g_2^* = \left(\frac{c}{a}\right)^2 \end{aligned}$$

We have determined there are two steady states: $g_1^* = 0\,,\, g_2^* = \left(\frac{c}{a}\right)^2$.

To determine $\lim_{t\to\infty} g(t)$, we check which of these steady states is stable.

Notice:

$$f(g) = cg^{1/2} - ag \implies f'(g) = \frac{c}{2g^{1/2}} - a$$

However, attempting to evaluate $f'(g)$ at g_1^* yields:

$$f'(g_1^*) = \left[\frac{c}{2\cdot\sqrt{g_1^*}} - a\right]_{g_1^*=0} = \frac{c}{0} - a$$

As this is clearly not defined, we can employ a graphical approach to evaluate the eigenvalue of g_1^* from its right-sided limit:

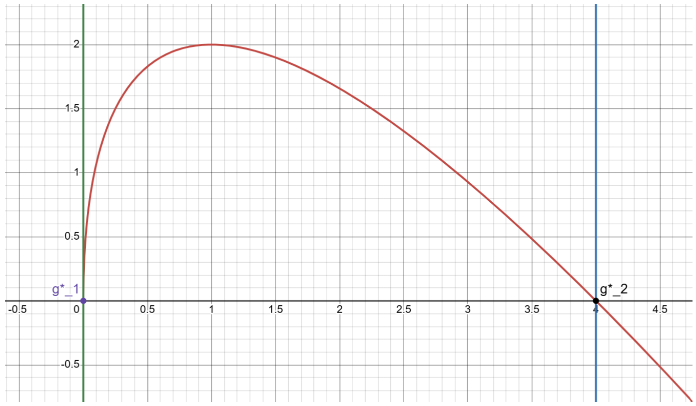

Figure 1: $f(g) = cg^{1/2} - ag$; a=2 c=4

Inspecting the gradient of $f(g)$ about both steady states, we can clearly notice that:

$$\left.\frac{df(g)}{dg}\right|_{g=0^+} > 0 \text{ and } \left.\frac{df(g)}{dg}\right|_{g=\frac{c^2}{a^2}} < 0$$

Specifically:

$$\left.\frac{df(g)}{dg}\right|_{g=\frac{c^2}{a^2}} = \left[\frac{c}{2\cdot\sqrt{g_2^*}} - a\right]_{g_2^*=\frac{c^2}{a^2}} = \frac{c}{2\cdot\frac{c}{a}} - a = \frac{a}{2} - \frac{2a}{2} = -\frac{a}{2} < 0.$$

Therefore, we can conclude that $g_1^* = 0$ is an unstable steady state, and $g_2^* = \frac{c^2}{a^2}$ is a stable steady state.

I.e. because we have shown that $g_2^* = \frac{c^2}{a^2}$ is a (and the only) stable steady state of the system, we have:

$$\lim_{t\to\infty} g(t) = \frac{c^2}{a^2} := g^* \quad \square$$

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Notice that since we are given $a, c > 0 \implies g^* > 0$ and therefore, our solution is biologically valid.

(b) Now solve the differential equation explicitly to find

$$g(t) = \frac{1}{a^2}\left(c - (c - ag_0^{1/2})e^{-at/2}\right)^2.$$

SOLUTION:

As hinted, we begin by making the substitution $g(t) = h^2(t)$ which yields:

$$\frac{dg(t)}{dt} = 2h(t)\frac{dh(t)}{dt}$$

So we have:

$$\frac{dg(t)}{dt} = cg^{1/2}(t) - ag(t) = ch(t) - ah^2(t) = 2h(t)\frac{dh(t)}{dt}$$

As we observed in Figure 1 for $f(g) = g'$:

$$\begin{cases} f(g) > 0 & ; \quad g \in (0, g^*) \\ f(g) < 0 & ; \quad g \in (g^*, \infty) \end{cases} \implies \begin{cases} g' > 0 \implies g(t) \in [g_0, g^*] & ; \quad 0 < g_0 < g^* \\ g' < 0 \implies g(t) \in [g^*, g_0] & ; \quad 0 < g^* < g_0 \end{cases} : t \geq 0$$

$$\implies g(t) \geq \min\{g_0, g^*\} > 0\,\forall t \geq 0 \implies g(t) \neq 0 \implies h(t) \neq 0.$$

Therefore, we can divide through by $h(t)$.

$$ch(t) - ah^2(t) = 2h(t)\frac{dh(t)}{dt} \implies c - ah(t) = 2\frac{dh(t)}{dt}$$

Applying separation of variables, we have:

$$dt = -2\frac{dh(t)}{ah(t) - c}$$

Integrating this expression then yields:

$$\int dt = -2\int \frac{dh(t)}{ah(t) - c}$$

$$\implies t = -\frac{2}{a}\ln|ah(t) - c| + \ln(\mathrm{k})$$

$$\implies -\frac{at}{2} = \ln|ah(t) - c| + \ln(\mathrm{k})$$

$$\implies e^{-\frac{at}{2}} = k \cdot (ah(t) - c)$$

Substituting $g(t) = h^2(t) \implies h(t) = \sqrt{g(t)}$ into our current expression:

$$e^{-\frac{at}{2}} = k \cdot (a\sqrt{g(t)} - c)$$

Now we can apply initial conditions ($t = 0$) to find k by evaluating:

$$e^{-\frac{at}{2}}\Big|_{t=0} = k \cdot (a\sqrt{g(t)} - c)\Big|_{t=0}$$

$$\implies 1 = k \cdot (a\sqrt{g_0} - c)$$

$$\implies k = \frac{1}{a\sqrt{g_0} - c}$$

Substituting this value of k back into our expression yields:

$$e^{-\frac{at}{2}} = \left(\frac{1}{a\sqrt{g_0} - c}\right) \cdot (a\sqrt{g(t)} - c)$$

Now, solving for $g(t)$:

$$(a\sqrt{g_0} - c)\, e^{-\frac{at}{2}} = a\sqrt{g(t)} - c$$

$$\implies (c - a\sqrt{g_0})\, e^{-\frac{at}{2}} = c - a\sqrt{g(t)}$$

$$\implies c - (c - a\sqrt{g_0})\, e^{-\frac{at}{2}} = a\sqrt{g(t)}$$

$$\implies \frac{1}{a}\left(c - (c - a\sqrt{g_0})\, e^{-\frac{at}{2}}\right) = \sqrt{g(t)}$$

$$\implies \frac{1}{a^2}\left(c - (c - a\sqrt{g_0})\, e^{-\frac{at}{2}}\right)^2 = g(t) \quad \square$$

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This matches the form of the proposed solution to this differential equation.

We can also notice that since our solution is in the form of a product of squares, this means $g(t) > 0\,\forall t \in [0, \infty)$ which confirms the solutions' biological validity.

(c) Verify that the equilibrium solution $g = \frac{c^2}{a^2}$ satisfies the differential equation.

SOLUTION:

Evaluating (LHS), if $g(t) = g = \frac{c^2}{a^2}$, then we have:

$$\frac{dg}{dt} = \frac{d}{dt}\left(\frac{c^2}{a^2}\right) = 0$$

Evaluating (RHS), if $g(t) = g = \frac{c^2}{a^2}$, then we have:

$$g^{1/2}(t) = \left(\frac{c^2}{a^2}\right)^{1/2} = \frac{c}{a}$$

$$\implies cg^{1/2}(t) - ag(t) = c\left(\frac{c}{a}\right) - a\left(\frac{c^2}{a^2}\right)$$

$$= \frac{c^2}{a} - \frac{c^2}{a} = 0$$

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I.e. (LHS) $= 0 =$ (RHS) confirming that the equilibrium solution $g = \frac{c^2}{a^2}$ satisfies the differential equation. $\square$

(d) Determine the value of $g(t)$ when $t = 0$ using the initial condition.

SOLUTION:

Applying our obtained solution to this system, and evaluating at $t = 0$, we have:

$$g(t)|_{t=0} = \frac{1}{a^2}\left(c - (c - a\sqrt{g_0})\, e^{-\frac{at}{2}}\right)^2\Big|_{t=0}$$

$$\implies g(0) = \frac{1}{a^2}\left(c - (c - a\sqrt{g_0})\, e^{-\frac{a\cdot 0}{2}}\right)^2$$

$$= \frac{1}{a^2}\left(c - (c - a\sqrt{g_0})\right)^2 = \frac{1}{a^2}\left(a\sqrt{g_0}\right)^2 = \frac{1}{a^2}\cdot a^2 \cdot g_0 = g_0$$

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I.e. we have confirmed that our solution for $g(t)$ respects the given initial condition: $g(t)|_{t=0} = g(0) = g_0$. $\square$

(e) Find the time t when the population size $g(t)$ reaches half of its equilibrium value.

SOLUTION:

We aim to solve the following equation for t:

$$g(t) = \frac{1}{2}\cdot\frac{c^2}{a^2}$$

We will need to be careful about how we approach this to ensure we don't get any biologically invalid solutions.

We can start with this stage of our working from (b):

$$(a\sqrt{g_0} - c)\, e^{-\frac{at}{2}} = a\sqrt{g(t)} - c \to (a\sqrt{g_0} - c)\, e^{-\frac{at}{2}} = a\sqrt{\frac{g^*}{2}} - c$$

$$\implies (a\sqrt{g_0} - c)\, e^{-\frac{at}{2}} = a\sqrt{\frac{c^2}{2a^2}} - c$$

We can now solve this for t:

$$(a\sqrt{g_0} - c)\, e^{-\frac{at}{2}} = \frac{c}{\sqrt{2}} - c$$

$$\implies e^{-\frac{at}{2}} = \frac{\frac{c}{\sqrt{2}} - c}{(a\sqrt{g_0} - c)} = \frac{c - \frac{c}{\sqrt{2}}}{(c - a\sqrt{g_0})}$$

To ensure a valid solution, we need to notice that $e^{-\frac{at}{2}} > 0\,\forall\, t$. Therefore, we must have:

$$\frac{c - \frac{c}{\sqrt{2}}}{(c - a\sqrt{g_0})} = \frac{c(1 - \frac{1}{\sqrt{2}})}{(c - a\sqrt{g_0})} > 0$$

Since $c > 0\,, 1 - \frac{1}{\sqrt{2}} > 0 \implies c(1 - \frac{1}{\sqrt{2}}) > 0$. So our condition requires:

$$(c - a\sqrt{g_0}) > 0 \iff g_0 < g^*$$

Next, because we only consider $t \in [0, \infty)$ to model a biologically valid system, on this domain we will have $0 < e^{-\frac{at}{2}} \leq 1$.

The lower bound has been ensured by the condition $g_0 < g^*$.

Now we check what conditions must be imposed to ensure $e^{-\frac{at}{2}} \leq 1$:

$$e^{-\frac{at}{2}} = \frac{c - \frac{c}{\sqrt{2}}}{(c - a\sqrt{g_0})} \leq 1$$

Because we have conditioned $g_0 < g^* \iff (c - a\sqrt{g_0}) > 0$, our inequality is unaffected by multiplication through by the denominator.

$$\implies c - \frac{c}{\sqrt{2}} \leq c - a\sqrt{g_0}$$

$$\implies \frac{c}{\sqrt{2}} \geq a\sqrt{g_0} \implies \frac{c^2}{2a^2} = \frac{g^*}{2} \geq g_0$$

So we have $g_0 \in \left(0, \frac{g^*}{2}\right]$ as our condition to ensure the solution, t remains biologically valid.

Note the following:

1. If $g_0 = \frac{g^*}{2}$ then $t = 0$ (this will be a result of the following form of t, and is trivial.
2. If $g_0 \in (\frac{g^*}{2}, g^*)$ then whilst the solution for t will exist, it requires $t < 0$ which is biologically invalid.
3. If $g_0 \in [g^*, \infty)$ then $g > g^*\,\forall t \implies \nexists\, t \in [0, \infty)$ such that $g(t) = \frac{g^*}{2}$.

We can now proceed to solve for t given our imposed conditions:

$$e^{-\frac{at}{2}} = \frac{c(1 - \frac{1}{\sqrt{2}})}{(c - a\sqrt{g_0})}$$

$$\implies e^{-\frac{at}{2}} = \frac{1 - \frac{1}{\sqrt{2}}}{(1 - \frac{a}{c}\sqrt{g_0})}$$

$$\implies -\frac{at}{2} = \ln\left(\frac{1 - \frac{1}{\sqrt{2}}}{(1 - \frac{a}{c}\sqrt{g_0})}\right)$$

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$$\implies t = \frac{2}{a}\ln\left(\frac{1-\frac{a}{c}\sqrt{g_0}}{1-\frac{1}{\sqrt{2}}}\right) \quad ; g_0 \in \left(0, \frac{g^*}{2}\right] \qquad \square$$

Figure 2 demonstrates the accuracy of this solution.

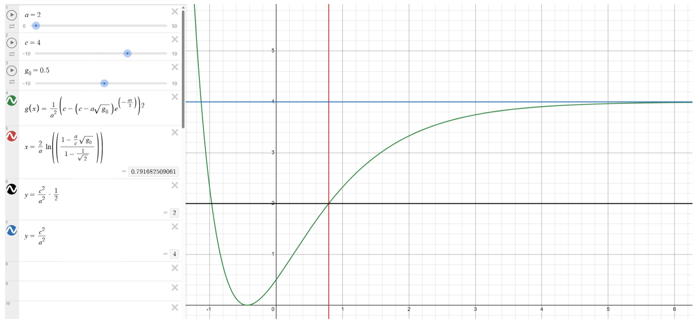

Figure 2: Intersection of $g(t)$ and half of the equilibrium value; $a = 2$, $c = 4$

(f) Discuss the effect of increasing the parameter a on the long-term behaviour of $g(t)$.

SOLUTION:

1) Decreased Equilibrium

The first effect of increasing a on the long-term behaviour of $g(t)$ is a decrease in the equilibrium value.

We have shown that the stable steady state / equilibrium of $g(t) = \frac{c^2}{a^2} = g^* > 0$.

Therefore, if $a \to ma$, $m > 0$, then:

$$g^* = \frac{c^2}{a^2} \to \frac{c^2}{(ma)^2} = \frac{1}{m^2}\left(\frac{c^2}{a^2}\right) = \frac{1}{m^2}\cdot g^*$$

I.e. increasing a by a factor of m will decrease the equilibrium by a factor of m^2.

2) Decreased recovery time.

The second effect of increasing a on the long-term behaviour of $g(t)$ is the system will experience a decrease in the recovery time.

As we saw previously,

$$f'(g^*) = -\frac{a}{2} \implies T_R\left(\frac{c^2}{a^2}\right) = \mathcal{O}\left(\frac{1}{f'(g^*)}\right) = \mathcal{O}\left(-\frac{2}{a}\right) = \frac{2}{a}$$

So, as a increases, the Recovery Time will decrease, inversely to a.

3) Increased equilibrium convergence rate.

By evaluating:

$$
\begin{aligned}
|g(t)-g^*| &= \left|\frac{1}{a^2}\Big(c-\big(c-a\sqrt{g_0}\big)e^{-\frac{a}{2}t}\Big)^2-\frac{c^2}{a^2}\right| \\
&= \left|\frac{1}{a^2}\left[-2c\big(c-a\sqrt{g_0}\big)e^{-\frac{a}{2}t}+\big(c-a\sqrt{g_0}\big)^2e^{-at}\right]\right| \\
&\leq \frac{1}{a^2}\left|\left[-2c\big(c-a\sqrt{g_0}\big)e^{-\frac{a}{2}t}\right]\right|+\frac{1}{a^2}\left|\left[\big(c-a\sqrt{g_0}\big)^2e^{-at}\right]\right| \\
&= \frac{2c\left|c-a\sqrt{g_0}\right|}{a^2}e^{-\frac{a}{2}t}+\frac{\big(c-a\sqrt{g_0}\big)^2}{a^2}\left(e^{-at}\right) \\
&\leq \frac{2c\left|c-a\sqrt{g_0}\right|}{a^2}e^{-\frac{a}{2}t}+\frac{\big(c-a\sqrt{g_0}\big)^2}{a^2}\left(e^{-\frac{a}{2}t}\right) \\
&= \frac{2c\left|c-a\sqrt{g_0}\right|+\big(c-a\sqrt{g_0}\big)^2}{a^2}e^{-\frac{a}{2}t} \\
&= C_a(c,g_0)e^{-\frac{a}{2}t}\to 0.
\end{aligned}
$$

we can see that g^* is exponentially stable with convergence rate $\frac{a}{2}$ and therefore, by increasing a, the rate at which $g(t)$ converges to g^* increases.

4) Change of trajectory direction towards g^*.

As we observed in (b):

$$\left(a\sqrt{g_0}-c\right)e^{-\frac{at}{2}}=\left(a\sqrt{g(t)}-c\right)$$

So we have that:

$$g'(t)=\sqrt{g(t)}\left(c-a\sqrt{g(t)}\right)=-\sqrt{g(t)}\left(a\sqrt{g(t)}-c\right)$$

$$=-\underbrace{\sqrt{g(t)}}_{>0}\left(\left(a\sqrt{g_0}-c\right)\underbrace{e^{-\frac{at}{2}}}_{>0}\right)$$

That is to say:

$$\operatorname{sgn}\left(g'(t)\right)=-\operatorname{sgn}\left(a-\sqrt{g_0}c\right)=\begin{cases}1 & ;\ a<\frac{c}{\sqrt{g_0}} \\ -1 & ;\ a>\frac{c}{\sqrt{g_0}}\end{cases} \quad :\forall\, t\in[0,\infty)$$

Meaning $g(t)$ is monotone on $[0,\infty)$ and given fixed values for c and g_0, g will approach $g^*=\frac{c^2}{a^2}$ from either above, or below depending on a. I.e. by increasing a, $g(t)$ will eventually become a strictly decreasing function that approaches g^* from above.

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Conclusion

We have shown in f(1, 2, 3, 4) that as the parameter a increases, $g(t)$ will approach an increasingly smaller equilibrium value, $g^*=\frac{c^2}{a^2}$ at an increasingly faster rate with decreasing recovery time, and, once a increases beyond a certain point $(\frac{c}{\sqrt{g_0}})$, $g(t)$ will become a decreasing function, approaching g^* from above. $\square$

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Well done!