Math 361 Winter 2001/2002
Assignment 4 - Solutions

1.Steady States, $N_{t+1} = N_t = N^*$:

$$N^* \left[\left(1 + e^{A(N^*-B)}\right)(1-\lambda_1) - \lambda_2 \right] = 0$$

This has the solutions

$$\begin{aligned} N^* &= 0 \\ N^* &= \frac{1}{A} \ln \frac{\lambda_1 + \lambda_2 - 1}{1 - \lambda_1} + B \end{aligned}$$

provided

$$\frac{\lambda_1 + \lambda_2 - 1}{1 - \lambda_1} > 0$$

and

$$\ln \frac{\lambda_1 + \lambda_2 - 1}{1 - \lambda_1} > -AB.$$

Computing the derivative of the function

$$F(N) = \left(\lambda_1 + \frac{\lambda_2}{1 + e^{A(N^*-B)}} \right) N,$$

it can be seen that

$$\begin{aligned} \frac{dF}{dN}\Big|_{N^*=0} &= \lambda_1 + \frac{\lambda_2}{1 + e^{-AB}} \\ \frac{dF}{dN}\Bigg|_{N^*=\frac{1}{A}\ln\frac{\lambda_1+\lambda_2-1}{1-\lambda_1}+B} &= 1 - \frac{(1-\lambda_1)(\lambda_1+\lambda_2-1)}{\lambda_2} \left(\ln \frac{\lambda_1 + \lambda_2 - 1}{1 - \lambda_1} + AB \right) \end{aligned}$$

Thus, if $\ln \frac{\lambda_1+\lambda_2-1}{1-\lambda_1} > -AB$, which is the condition for the second equilibrium to exist, then $\frac{dF}{dN}|_{N^*=0} > 1$, hence $N^* = 0$ is unstable. In this case the other equilibrium is stable if

$$\left| 1 - \frac{(1-\lambda_1)(\lambda_1+\lambda_2-1)}{\lambda_2} \left(\ln \frac{\lambda_1 + \lambda_2 - 1}{1 - \lambda_1} + AB \right) \right| < 1$$

and unstable otherwise. For example, if λ_1 is very small, then for given A and B the second equilibrium becomes unstable if λ_2 is large enough. If $\ln \frac{\lambda_1+\lambda_2-1}{1-\lambda_1} < -AB$ then $N^* = 0$ is the only equilibrium, and it is stable.

2. a. In a population of size x the per capita number of offspring is

$$f(x) = \frac{\lambda}{(1+x)^b}.$$

This function is monotone decreasing with $f(0) = \lambda$ and $f(x) \to 0$ for $x \to \infty$. The decrease in per capita number of offspring occurs more abruptly for higher values of b. For $b > 1$ the function has a single inflection point.

b. The case $b = 1$ was discussed in class. For $b > 1$ the function

$$F(x) = f(x) \cdot x = \frac{\lambda x}{(1+x)^b}$$

has a single maximum, with $F(0) = 0$ and $F(x) \to 0$ for $x \to \infty$ with a single inflection point.

c. The carrying capacity is that population size x^* for which the per capita number of offspring is exactly 1, i.e. for which $f(x^*) = 1$. At the carrying capacity, the population simply replaces itself in each year, hence the name. Thus the carrying capacity is simply the positive equilibrium of the function $F(x)$, i.e. the solution x^* of

$$F(x^*) = x^*$$

with $x^* > 0$. This solution is given by

$$x^* = \lambda^{1/b} - 1.$$

d. A straightforward calculation shows that

$$\frac{dF}{dx}(x^*) = 1 - b(1 - \frac{1}{\lambda^{1/b}}).$$

e. Cobwebbing illustrates the stability of the carrying capacity depending on the parameter values.

3.

a. For $\lambda = 2$, there is a monotonic approach to equilibrium.

b. For $\lambda = 5$, the population reaches an equilibrium via dampened oscillations

c. For $\lambda = 10$, the population enters a two cycle.

d. For $\lambda = 20$, the population enters a four cycle.

e. For $\lambda = 40$, the population exhibits chaotic dynamics.

4.

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

For large $x(t)$, $1 + x(t) \approx x(t)$, thus $\ln \frac{x(t)}{x_s(t)} = b \ln(x(t))$ for large $x(t)$. 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 random sample of $x(t)$, that is the number of individuals in the population at time t. Then take a corresponding sample of the number of individuals that survive to reproduction, $x_s(t)$. Regress the $\ln(x_s(t))$ on $\ln(x(t))$: the slope of the regression line will give an estimate of b.

5. All of the data points except one lie below the curve defined by $-2 < -b(1 - \frac{1}{\lambda^{1/b}})$. This implies that all except one species have demographic parameters inducing a stable equilibrium. The species that has demographic parameters leading to instability is the one corresponding to the point (75.0,3.4), i.e. the Potato Beetle.

6.

a. 2. Note that there is 3rd equilibrium at 0.

b. The larger of the equilibrium refereed to in part a. is stable, the lower one unstable. (Note that the equilibrium 0 is also stable, due to the Allee effect.)

c. If the perturbation is to smaller values than the equilibrium value, then the population will converge towards 0, i.e. go extinct. If the perturbation is to larger values than the equilibrium value, then the population will converge toward the upper equilibrium, i.e. towards the carrying capacity.

7. a. S is a steady state: $F(S) = S$. C is an unstable steady state A and B are two points representing a steady limit cycle. The system will oscillate between points A and B in the long term.

b. As an ecosystem is enriched $F(n_k)$ becomes elevated. This corresponds to making the $y = x$ on an individual plot shallower and shallower. During this process, the steady state S moves from its original position to the left of the maximum of the function F towards positions further to the right, and hence towards positions at which the derivative of F becomes more and more negative. Thus, due to enrichment the derivative of F at S eventually becomes smaller than -1, so that the equilibrium S is unstable.

8. a. An additional constraint can be derived by forcing the eigenvalues to be real. Thus

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

We already know that $\beta^2 < 4$ so

$$\begin{aligned} 4 - 4\gamma > \beta_2 - 4\gamma &> 0 \\ 4 &> 4\gamma \\ 1 &> \gamma \end{aligned}$$

Thus $1 + \gamma < 2$ and so $2 > 1 + \gamma > |\beta|$.

b. If $\frac{\beta}{2} < 0$, then

$$\begin{aligned} -1 + \frac{\beta}{2} &> -\frac{\sqrt{\beta^2 - 4\gamma}}{2} \\ 1 - \beta + \frac{\beta^2}{4} &> \frac{\beta^2}{4} - \gamma \\ 1 + \gamma &> \beta \end{aligned}$$

All other conditions are equivalent.

c. If we have complex eigenvalues $\lambda_{1/2} = a \pm bi$ then $\beta^2 - 4\gamma < 0$, and

$$\begin{aligned} a &= \frac{\beta}{2} \\ b &= \frac{\sqrt{4\gamma - \beta^2}}{2} \end{aligned}$$

and

$$|\lambda_1| = |\lambda_2| = \left(a^2 + b^2\right)^{\frac{1}{2}} = \left(\left(\frac{\beta}{2}\right)^2 + \gamma - \left(\frac{\beta}{2}\right)^2\right)^{\frac{1}{2}} = \sqrt{\gamma}$$

Hence $\left|\lambda_{1/2}\right| < 1 \Leftrightarrow \sqrt{\gamma} < 1 \iff \gamma < 1 \iff \gamma + 1 < 2$. Also note that $4\gamma > \beta^2 \iff 2\sqrt{\gamma} > |\beta|$. Now $2\sqrt{\gamma} < \sqrt{\gamma} + 1 \iff \sqrt{\gamma} < 1$, which implies the claim.

9. a. Steady state $p(t+1) = p(t) = p^*$:

$$\begin{aligned} p^* &= \frac{p^* w_A}{p^* w_A + (1 - p^*) w_B} \\ p^* \left(p^* \left(w_A - w_B\right) - \left(w_A - w_B\right)\right) &= 0 \end{aligned}$$

Provided $w_A \neq w_B$, this equation has $p^* = 0$ and $p^* = 1$ as the only solutions. To test for local stability we calculate the derivative of

$$F(p) = \frac{p w_A}{p w_A + (1-p) w_B} :$$

$$\frac{dF}{dp} = \frac{w_A w_B}{\left(p w_A + (1-p) w_B\right)^2}$$

Thus

$$\frac{dF}{dp}|_{p=0} = \frac{w_A}{w_B}$$

and

$$\frac{dF}{dp}|_{p=1} = \frac{w_B}{w_A}$$

If $|w_A| > |w_B|$ then $p = 0$ is unstable and $p = 1$ is stable. If $|w_A| < |w_B|$ then $p^* = 0$ is stable and $p^* = 1$ is unstable.

b. Even though the conditions for stability derived in part a. are only local conditions, it can be seen that in this case these conditions are actually global, in the sense that not only starting conditions close to the stable equilibrium will converge to the stable equilibrium, but in fact all starting conditions (with the exception of the other equilibrium of course!) will converge towards the stable equilibrium, i.e. towards $p^* = 0$ or $p^* = 1$ depending on the relative magnitude of w_A and w_B (note that only starting conditions in the interval $[0, 1]$ make biological sense, since the variable p is a frequency and hence must be ≥ 0 and □ 1). The reason is simply that the function F either lies above the diagonal for all values of $p \in [0, 1]$, or it lies below the diagonal for these values, depending on the relative magnitude of w_A and w_B. In the first of these cases, $p^* = 0$ is unstable, and cobwebbing immediately shows that the system converges to $p^* = 1$ independent of the starting condition (as long as the starting condition is not $p(0) = 0$). In the second case, $p^* = 1$ is unstable, and cobwebbing immediately shows that the system converges to $p^* = 0$ independent of the starting condition (as long as the starting condition is not $p(0) = 0$).