

Math 361 Winter 2001/2002
Assignment 5 - Solutions

1. This is explained in the textbook on page 48 and 49 (top). Calculating the derivative df/dx at the two points x_1 and x_2 of the 2-cycle yields

$$\frac{dg}{dx}(x_1) = \frac{dg}{dx}(x_2) = \frac{df}{dx}(x_1) \cdot \frac{df}{dx}(x_2) = 4 + 2r - r^2$$

for $r \geq 3$. The 2-cycle is stable if and only if

$$\left| \frac{df}{dx}(x_1) \cdot \frac{df}{dx}(x_2) \right| = |4 + 2r - r^2| < 1,$$

if and only if $3 < r < 1 + \sqrt{6}$. (Note that this last value differs slightly for the value given in the book.)

2. Equilibria of

$$\begin{aligned} p(t+1) &= f(p(t)) \\ &= \frac{p(t) \cdot (a - p(t))}{p(t) \cdot (a - p(t)) + (1 - p(t)) \cdot (b + p(t))} \end{aligned}$$

are solutions of $p^* = f(p^*)$:

$$\begin{aligned} p^* &= \frac{p^* (a - p^*)}{p^* (a - p^*) + (1 - p^*) (b + p^*)} \\ p^* &= 0 \\ 2p^{*2} - 3p^* + 1 &= 0 \\ p^* &= \frac{1}{2}, 1 \end{aligned}$$

$$f'(p) = \frac{(a - 2p) [(b + 2p - 2p^2) - 2p(a - p)]}{(p(a - p) + (1 - p)(b + p))^2}$$

$$\begin{aligned} f'(0) &= \frac{a}{a - 1} \\ f'(1) &= \frac{a}{a - 1} \\ f'\left(\frac{1}{2}\right) &= \frac{2a - 2}{2a - 1} \end{aligned}$$

Since $a > 1$, $\frac{a}{a-1} > 1$ as well, and so 0 and 1 are unstable. Also, since $a > 1$, $2a - 2$ and $2a - 1$ are both > 0 , and hence $\frac{2a-2}{2a-1} < 1$. Thus, $p^* = \frac{1}{2}$ is stable.

Plotting the function f shows that $f(p) \leq p$ for $0 \leq p \leq 1/2$ and $f(p) \geq p$ for $1/2 \leq p \leq 1$. Cobwebbing therefore shows that $\lim_{t \rightarrow \infty} p(t) = 1/2$ as long

as $p(0) \neq 0, 1$. Thus, this genetic system converges to a polymorphism in which both types are equally abundant. This results from the fact that both types have a fitness advantage when rare, and that the fitness functions are symmetric about the vertical line at $p = 1/2$.

3. (a)

$$f(x, y) = \sin(x^2 + y^2)$$

$$\frac{\partial f}{\partial x} = 2x \cos(x^2 + y^2)$$

$$\frac{\partial f}{\partial y} = 2y \cos(x^2 + y^2)$$

(b)

$$g(x, y) = \cos x^3 \cdot e^{-xy}$$

$$\frac{\partial g}{\partial x} = -e^{-xy} (y \cos x^3 + 3x^2 \sin x^3)$$

$$\frac{\partial g}{\partial y} = -xe^{-xy} \cos x^3$$

(c)

$$f(x, y) = x^n + x^{n-1}y + x^{n-2}y^2 + \dots + x^2y^{n-2} + xy^{n-1} + y^n$$

$$\frac{\partial f}{\partial x} = nx^{n-1} + (n-1)x^{n-2}y + (n-2)x^{n-3}y^2 + \dots + 2xy^{n-2} + y^{n-1}$$

$$\frac{\partial f}{\partial y} = x^{n-1} + 2x^{n-2}y + \dots + (n-2)x^2y^{n-3} + (n-1)xy^{n-2} + ny^{n-1}$$

(d)

$$h(x, y) = \frac{xy^3 + 4y^2}{x^4 + 7y}$$

$$\frac{\partial h}{\partial x} = \frac{y^3(x^4 + 7y) - (4x^4y^3 + 16x^3y^2)}{(x^4 + 7y)^2}$$

$$\frac{\partial h}{\partial y} = \frac{3x^5y^2 + 8x^4y + 14xy^3 + 28y^2}{(x^4 + 7y)^2}$$

(e)

$$g(x, y) = \ln(\cos -xy)$$

$$\frac{\partial g}{\partial x} = y \tan -xy$$

$$\frac{\partial g}{\partial y} = x \tan -xy$$

(f)

$$f(x, y, z) = xyz + (xyz)^2$$

$$\frac{\partial f}{\partial x} = yz(1 + 2xyz)$$

$$\frac{\partial f}{\partial y} = xz(1 + 2xyz)$$

$$\frac{\partial f}{\partial z} = xy(1 + 2xyz)$$

(g)

$$f(x, y, z) = e^{-(x^2+y^2+z^2)}$$

$$\frac{\partial f}{\partial x} = -2xe^{-(x^2+y^2+z^2)}$$

$$\frac{\partial f}{\partial y} = -2ye^{-(x^2+y^2+z^2)}$$

$$\frac{\partial f}{\partial z} = -2ze^{-(x^2+y^2+z^2)}$$

4. Under the assumptions we have:

$$\begin{aligned}\frac{\partial F}{\partial x} &= e^{1-x-ay}(1-x) \\ \frac{\partial F}{\partial y} &= -axe^{1-x-ay} \\ \frac{\partial G}{\partial x} &= 1 - e^{-ay} \\ \frac{\partial G}{\partial y} &= axe^{-ay}\end{aligned}$$

Thus the Jacobian J at the equilibrium is

$$J = \begin{pmatrix} e^{1-x^*-ay^*}(1-x^*) & -ax^*e^{1-x^*-ay^*} \\ 1 - e^{-ay^*} & ax^*e^{-ay^*} \end{pmatrix}.$$

Note that at equilibrium $1 - x^* - ay^* = 0$, which results from assuming that $x^* \neq 0$ in the first equation and solving. Thus the Jacobian becomes

$$J = \begin{pmatrix} 1 - x^* & -ax^* \\ 1 - e^{-ay^*} & ax^*e^{-ay^*} \end{pmatrix}.$$

Let's look at the equilibrium equations

$$\begin{aligned}x^* &= x^* \exp[1 - x^* - ay^*] \\ y^* &= x^*(1 - \exp[-ay^*])\end{aligned}$$

From $1 - x^* - ay^* = 0$ we conclude that $x^* < 1$ and $ay^* < 1$ (because $a, y^* > 0$). From the second of the above equations it then follows that $y^* < x^* < 1$ as well. As a consequence, if a is sufficiently small then $ay^* \approx 0$, which implies that $e^{-ay^*} \approx 1 - ay^*$. Thus, as a becomes small the Jacobian becomes

$$J = \begin{pmatrix} 1 - x^* & -ax^* \\ ay^* & ax^*(1 - ay^*) \end{pmatrix}.$$

Also, as a becomes small terms containing a^2 can be omitted, so $-ax^*(1 - ay^*) = -ax^*$, and using again $1 - x^* - ay^* = 0$ the Jacobian becomes

$$J = \begin{pmatrix} 1 - x^* & -ax^* \\ 1 - x^* & ax^* \end{pmatrix}.$$

As a goes to 0 the entries in the right column go to 0 because $x^* < 1$, and the entries in the left column go to 0 because $1 - x^* - ay^* = 0$, and because ay^* goes to 0. Thus, as a goes to 0 the matrix J converges to the matrix with all entries equal to 0, and hence with all eigenvalues equal to 0 as well. In particular, as a goes to 0 the dominant eigenvalue of J has absolute value smaller than 1.

5.

$$\begin{aligned} H_{t+1} &= FH_t \left(1 + \frac{aP_t}{k}\right)^{-k} \\ P_{t+1} &= H_t \left(1 - \left(1 + \frac{aP_t}{k}\right)^{-k}\right) \end{aligned}$$

$(H, P) = (0, 0)$ and $(H, P) = \left(\frac{kF(F^{1/k}-1)}{a(F-1)}, \frac{k(F^{1/k}-1)}{a}\right)$ are both steady states of this system.

Stability:

$$\begin{aligned} \frac{\partial f}{\partial H} &= F \left(1 + \frac{aP}{k}\right)^{-k} \\ \frac{\partial f}{\partial P} &= -aFH \left(1 + \frac{aP}{k}\right)^{-k-1} \\ \frac{\partial g}{\partial H} &= 1 - \left(1 + \frac{aP}{k}\right)^{-k} \\ \frac{\partial g}{\partial P} &= aH \left(1 + \frac{aP}{k}\right)^{-k-1} \end{aligned}$$

Thus the Jacobian J is

$$J = \begin{pmatrix} F \left(1 + \frac{aP}{k}\right)^{-k} & -aFH \left(1 + \frac{aP}{k}\right)^{-k-1} \\ 1 - \left(1 + \frac{aP}{k}\right)^{-k} & aH \left(1 + \frac{aP}{k}\right)^{-k-1} \end{pmatrix}.$$

Evaluated at the equilibrium $(0, 0)$, this reduces to

$$J(0, 0) = \begin{pmatrix} F & 0 \\ 0 & 0 \end{pmatrix}.$$

Clearly, the eigenvalues of this matrix are F and 0, and so the equilibrium $(0, 0)$ is stable if and only if $F < 1$.

At the other equilibrium $(H, P) = \left(\frac{kF(F^{1/k}-1)}{a(F-1)}, \frac{k(F^{1/k}-1)}{a}\right)$, the Jacobian J becomes, after some algebra:

$$J = \begin{pmatrix} 1 & \frac{kF}{F-1} (F^{-1/k} - 1) \\ \frac{F-1}{F} & \frac{k}{F-1} (1 - F^{-1/k}) \end{pmatrix}.$$

Note that the parameter a does not appear in J and hence is not important for stability! In general, the magnitudes of the absolute values of the eigenvalues of this matrix depend on the parameter F and k . We know from problem 6 in assgnmt 4 that the equilibrium is stable if and only if

$$2 > 1 + \det(J) > |\text{tr}(J)|.$$

Now

$$\begin{aligned} \det(J) &= 1 \cdot \frac{k}{F-1} \left(1 - F^{-1/k}\right) - \frac{F-1}{F} \cdot \frac{kF}{F-1} \left(F^{-1/k} - 1\right) \\ &= \frac{kF}{F-1} \left(1 - F^{-1/k}\right) \end{aligned}$$

and

$$\begin{aligned} \text{tr}(J) &= 1 + \frac{k}{F-1} \left(1 - F^{-1/k}\right) \\ &= 1 + \det(J)/F \end{aligned}$$

Assuming $F > 1$ (so that the prey population is viable in the absence of the predator, and hence so that the equilibrium $(0, 0)$ becomes unstable) we see that $\det(J) > 0$, and hence that $1 + \det(J) > 1 + \det(J)/F$ (again because $F > 1$), so that the right hand of the above inequality is always satisfied. The left hand inequality is satisfied if $1 > \det(J)$, i.e. if

$$1 > \frac{k}{1-F} \left(1 - F^{-1/k}\right).$$

By taking the derivative of the function $h(k) = \frac{k}{1-F} (1 - F^{-1/k})$ one can check that $h(k)$ is a monotonically increasing function of k for all k with $0 < k < \infty$. Moreover, $h(1) = 1$. It follows that the equilibrium is stable if and only if $k < 1$.

6. (a) The number of radioactive decays in a given time interval, the number of defects in a product from production line. A more biological example - the number of tumors found in a mouse after injection with stem cells.

(b) This is simply a negative exponential.

(c) For the expected value of a random variable r following a Poisson distribution $p(r) = \frac{e^{-\mu} \mu^r}{r!}$ we get

$$\begin{aligned} E(r) = \sum_{r=0}^{\infty} r p(r) &= \sum_{r=0}^{\infty} \frac{r e^{-\mu} \mu^r}{r!} \\ &= \mu e^{-\mu} \sum_{r=1}^{\infty} \frac{\mu^{r-1}}{(r-1)!} \\ &= \mu e^{-\mu} e^{\mu} \\ &= \mu \end{aligned}$$

Thus, for the predator-prey system the parameter μ should be the expected number of predator encounter per prey individual. Now, the total number of N_e of encounters between prey and predator is, according to what is usually called the 'mass action principle', simply proportional to the number of prey and proportional to the number of predator individuals present, i.e. proportional to the product NP , with the proportionality reflecting the searching efficiency a of the predator. Thus $N_e = aNP$, and hence the per prey capita number of encounters is $\mu = N_e/N = aP$.

(d) The chance of encountering a single predator is $e^{-aP_t} \cdot aP_t$, and the chance of encountering at least 2 predator individuals is $1 - e^{-aP_t} - e^{-aP_t} \cdot aP_t = 1 - e^{-aP_t} (1 + aP_t)$. Therefore, the second equation would change as follows:

$$P_{t+1} = acN_t P_t e^{-aP_t} + 2cN_t (1 - e^{-aP_t} (1 + aP_t))$$

7. (a) The equations become

$$\begin{aligned} n_{t+1} &= \lambda n_t e^{-p_t} \\ p_{t+1} &= n_t (1 - e^{-p_t}) \end{aligned}$$

Only one parameter - λ !

(b) p_t is the effective number of parasites. Each of the rescaled number of hosts n_t gives rise to exactly one predator if encountered by a predator.

(c) Is $\beta^2 - 4\gamma < 0$?

We know that $\gamma > 1$ for all $\lambda > 1$ (see page 82 in the textbook). Therefore it is sufficient to find out whether $\beta^2 < 4$, which is the same as asking whether $\beta < 2$ since $\beta > 0$.

So is $1 + \frac{\ln \lambda}{\lambda - 1} < 2$? This is the same as asking if

$$S(\lambda) = \lambda - 1 - \ln \lambda > 0$$

Well $S(1) = 0$ and $S'(\lambda) \geq 0$ for all $\lambda \geq 1$, hence S is an increasing function of λ for $\lambda \geq 1$. Therefore, $S(\lambda) > 0$ for all $\lambda > 1$. Thus, the eigenvalues of the Jacobian matrix at the unstable equilibrium are not real, and hence we have a spiral instability with increasing oscillations away from the equilibrium.

8. (a) In a refuge of size EK , in which K is the carrying capacity of the population and E is the probability an individual is in the refuge when the population is at its carrying capacity, EK is the maximum size of the refuge. If every individual is equally likely to enter the refuge, and $EK \ll N(t)$, then $EK/N(t)$ is the probability an individual is in the refuge.

(b) If all individuals that are in the refuge escape parasitism, then the probability of escaping parasitism is 1. Of those that do not escape parasitism, the probability of being parasitized is $\exp[-aP(t)]$. Thus the expected probability an individual escapes parasitism is the probability it is in a refuge, $(EK/N(t))$, times the probability it escapes parasitism given it is in a refuge, (1), plus the

probability it is outside a refuge, $(1 - EK/N(t))$, times the probability of escaping parasitism given it is outside a refuge, $(\exp[-aP(t)])$. Together this is

$$\left(\frac{EK}{N(t)}\right) + \left(1 - \left(\frac{EK}{N(t)}\right)\right) (\exp[-aP(t)]).$$

(c) It follows from (b) that

$$\begin{aligned} N(t+1) &= \lambda N(t) \cdot \left(\frac{EK}{N(t)}\right) + \left(1 - \left(\frac{EK}{N(t)}\right)\right) (\exp[-aP(t)]) \\ &= \lambda N(t) \frac{EK}{N(t)} + \lambda N(t) \left(1 - \frac{EK}{N(t)}\right) \exp(-aP(t)) \\ &= \lambda EK + \lambda (N(t) - EK) \exp(-aP(t)). \end{aligned}$$

(d) The probability of not escaping parasitism is 1 minus the probability of escaping parasitism or,

$$\begin{aligned} &1 - \left(\left(\frac{EK}{N(t)}\right) + \left(1 - \left(\frac{EK}{N(t)}\right)\right) \exp[-aP(t)]\right) \\ &= \left(1 - \left(\frac{EK}{N(t)}\right)\right) (1 - \exp[-aP(t)]) \end{aligned}$$

Thus, the number of new predators generated on average by one prey individual is $c \cdot \left(1 - \left(\frac{EK}{N(t)}\right)\right) (1 - \exp[-aP(t)])$, hence

$$P(t+1) = cN(t) \left(1 - \left(\frac{EK}{N(t)}\right)\right) (1 - (\exp[-aP(t)])).$$

Simplification yields the desired result.

9. (a) The parameter m should be between 0 and 1 because interference among parasitoids should decrease the expected number of hosts parasitized by the parasitoid population. The term $aP(t)$ in $\exp(-aP(t))$ is the expected number of predators encountered by one prey individual (see problem 6 above). By raising $aP(t)$ to a power between 0 and 1, this expected number is reduced.

(b)

$$\begin{aligned} N(t+1) &= f(N(t), P(t)) = \lambda N(t) \exp\left[-(aP(t))^{1-m}\right] \\ P(t+1) &= g(N(t), P(t)) = cN(t)(1 - \exp\left[-(aP(t))^{1-m}\right]) \end{aligned}$$

(c) Equilibrium states (x, y) with $x, y > 0$:

$x = \lambda x \exp(-(ay)^{1-m})$, hence $\frac{1}{\lambda} = \exp(-(ay)^{1-m})$, $(ay)^{1-m} = \ln \lambda$, $ay = (\ln \lambda)^{1/(1-m)}$ and hence

$$y = \frac{(\ln \lambda)^{1/(1-m)}}{a}.$$

Now solve for x using the equation $y = cx(1 - \exp(-(ay)^{1-m}))$:

$$\frac{(\ln \lambda)^{1/(1-m)}}{a} = cx(1 - \exp(-\left(a \frac{(\ln \lambda)^{1/(1-m)}}{a}\right)^{1-m})) = cx(1 - \exp(-\ln \lambda)) = cx(1 - 1/\lambda), \text{ hence}$$

$$x = \frac{\lambda(\ln \lambda)^{1/(1-m)}}{ca(\lambda - 1)}$$

For $\lambda > e^1$ and $0 < m < 1$, the model with interference causes both the parasitoid and host to have higher equilibrium population sizes. For $1 < \lambda \leq e^1$ and $0 < m < 1$, interference causes both the parasitoid and the host to have lower equilibrium population sizes.

(d) Stability: A rather tedious calculation (best done using a computer algebra system!) shows that if m is close to 1, i.e. if interference is strong, then the equilibrium calculated in (c) becomes stable. Thus, interference can stabilize predator-prey population dynamics.