Math 361 Winter 2001/2002
Assignment 8 - Solutions

1. Steady states are found by solving the equations

$$\begin{aligned} x_1\,(1 - x_1 - \alpha_{12}x_2) &= 0 \\ x_2\,(1 - x_2 - \alpha_{21}x_1) &= 0 \end{aligned}$$

From equation 1, we see that $x_1 = 0 \implies x_2(1 - x_2) = 0 \implies x_2 = 0, 1$. Also, from equation 2 $x_2 = 0 \implies x_1 = 0, 1$. The final case occurs when $\alpha_{12}\alpha_{21} \neq 1$. Here

$$\begin{aligned} x_1 &= 1 - \alpha_{12}x_2 \\ \implies x_2 &= \frac{\alpha_{21} - 1}{\alpha_{12}\alpha_{21} - 1} \\ \implies x_1 &= \frac{\alpha_{12} - 1}{\alpha_{12}\alpha_{21} - 1} \end{aligned}$$

For this steady state to be positive (i.e. $x_1 > 0$ and $x_2 > 0$) we need either $\alpha_{12} > 1$ and $\alpha_{21} > 1$ or $\alpha_{12} < 1$ and $\alpha_{21} < 1$. Thus steady states for the system are found at $(0, 0), (0, 1), (1, 0), \left(\frac{\alpha_{12}-1}{\alpha_{12}\alpha_{21}-1}, \frac{\alpha_{21}-1}{\alpha_{12}\alpha_{21}-1}\right)$.

Stability analysis:

$$\begin{aligned} \frac{\partial f}{\partial x} &= 1 - 2x_1 - \alpha_{12}x_2 \\ \frac{\partial f}{\partial y} &= \alpha_{12}x_1 \\ \frac{\partial g}{\partial x} &= \alpha_{21}x_2 \\ \frac{\partial g}{\partial y} &= 1 - 2x_2 - \alpha_{21}x_1 \end{aligned}$$

Computing Jacobians:

$$J(0, 0) = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}$$

$\beta = 2, \gamma = 1$. So $(0, 0)$ is an unstable node.

$$J(0, 1) = \begin{pmatrix} 1 - \alpha_{12} & 0 \\ -\alpha_{21} & -1 \end{pmatrix}$$

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$\beta = -\alpha_{12} < 0, \gamma = \alpha_{12} - 1$. Therefore, $(0, 1)$ is locally stable if and only if $\alpha_{12} > 1$.

$$J(1,0) = \begin{pmatrix} -1 & -\alpha_{12} \\ 0 & 1 - \alpha_{21} \end{pmatrix}$$

$\beta = -\alpha_{21} < 0, \gamma = \alpha_{21} - 1$. Therefore, $(0, 1)$ is locally stable if and only if $\alpha_{21} > 1$.

$$J\left(\frac{\alpha_{12} - 1}{\alpha_{12}\alpha_{21} - 1}, \frac{\alpha_{21} - 1}{\alpha_{12}\alpha_{21} - 1}\right) = \begin{pmatrix} \frac{1-\alpha_{12}}{\alpha_{12}\alpha_{21}-1} & \frac{\alpha_{12}(1-\alpha_{12})}{\alpha_{12}\alpha_{21}-1} \\ \frac{\alpha_{21}(1-\alpha_{21})}{\alpha_{12}\alpha_{21}-1} & \frac{1-\alpha_{21}}{\alpha_{12}\alpha_{21}-1} \end{pmatrix}$$

$\beta = \frac{(1-\alpha_{12})+(1-\alpha_{21})}{\alpha_{12}\alpha_{21}-1}$, $\gamma = -\frac{(1-\alpha_{12})(1-\alpha_{21})}{\alpha_{12}\alpha_{21}-1}$. Therefore, $\left(\frac{\alpha_{12}-1}{\alpha_{12}\alpha_{21}-1}, \frac{\alpha_{21}-1}{\alpha_{12}\alpha_{21}-1}\right)$ is stable if and only if $\alpha_{12} < 1$ and $\alpha_{21} < 1$.

2. In the following, β denotes the trace of the Jacobian under consideration, and γ denotes its determinant. Steady states are classified according to the signs of β and γ, as explained on p. 190 in the textbook.

(a)

$$\begin{aligned} \frac{dx}{dt} &= y^2 - x^2 \\ \frac{dy}{dt} &= x - 1 \end{aligned}$$

Steady states:

$$\begin{aligned} x^2 &= y^2 \\ x &= 1 \implies y = \pm 1 \end{aligned}$$

Steady states at $(1, -1); (1, 1)$.
Jacobian:

$$J(x, y) = \begin{pmatrix} -2x & 2y \\ 1 & 0 \end{pmatrix}$$

Therefore

$$J(1, -1) = \begin{pmatrix} -2 & -2 \\ 1 & 0 \end{pmatrix}$$

$\beta = -2, \gamma = 2$. So this is a stable spiral.

$$J(1, 1) = \begin{pmatrix} -2 & 2 \\ 1 & 0 \end{pmatrix}$$

$\beta = -2, \gamma = -2$. So this is a saddle point.

(b)

$$\begin{aligned}\frac{dx}{dt} &= xy(y-1) \\ \frac{dy}{dt} &= x - y\end{aligned}$$

Steady states:

$$\begin{aligned}xy(y-1) &= 0 \\ x &= y \\ x &= 0 \implies y = 0 \\ y &= 1 \implies x = 1\end{aligned}$$

Steady states at $(0,0); (1,1)$.
Jacobian:

$$J(x,y) = \begin{pmatrix} y(y-1) & 2xy - x \\ 1 & -1 \end{pmatrix}$$

Therefore

$$J(0,0) = \begin{pmatrix} 0 & 0 \\ 1 & -1 \end{pmatrix}$$

$\beta = -1, \gamma = 0$. So this is a stable node.

$$J(1,1) = \begin{pmatrix} 0 & 1 \\ 1 & -1 \end{pmatrix}$$

$\beta = -1, \gamma = -1$. So this is a saddle point.

(c)

$$\begin{aligned}\frac{dx}{dt} &= x^2 + y \\ \frac{dy}{dt} &= -y\end{aligned}$$

Steady states:

$$\begin{aligned}x^2 + y &= 0 \\ y &= 0 \implies x = 0\end{aligned}$$

Steady state at $(0,0)$.

Jacobian:

$$J(x,y) = \begin{pmatrix} -2x & 1 \\ 0 & -1 \end{pmatrix}$$

Therefore

$$J(0,0) = \begin{pmatrix} 0 & 1 \\ 0 & -1 \end{pmatrix}$$

$\beta = -1, \gamma = 0$. So this is a stable node.

(d)

$$\begin{aligned} \frac{dx}{dt} &= -xy \\ \frac{dy}{dt} &= (1+x)(1-y) \end{aligned}$$

Steady states:

$$\begin{aligned} xy &= 0 \implies x = 0, y = 0 \\ x &= 0 \implies y = 1 \\ y &= 0 \implies x = -1 \end{aligned}$$

Steady states at $(0,1); (-1,0)$.
Jacobian:

$$J(x,y) = \begin{pmatrix} -y & -x \\ 1-y & -(1+x) \end{pmatrix}$$

Therefore

$$J(0,1) = \begin{pmatrix} -1 & 0 \\ 0 & -1 \end{pmatrix}$$

$\beta = -2, \gamma = 1$. So this is a stable node.

$$J(-1,0) = \begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix}$$

$\beta = 0, \gamma = -1$. So this is a saddle point.

(e)

$$\begin{aligned} \frac{dx}{dt} &= x^2 - y \\ \frac{dy}{dt} &= y^2 - x \end{aligned}$$

Steady states:

$$
\begin{aligned}
y &= x^2 \\
\Longrightarrow x(x^3-1) &= 0 \\
\Longrightarrow x &= 0 \Longrightarrow y = 0 \\
\Longrightarrow x &= 1 \Longrightarrow y = \pm 1
\end{aligned}
$$

Steady states at $(0,0), (1,-1), (1,1)$.
Jacobian:

$$
J(x,y) = \begin{pmatrix} 2x & -1 \\ -1 & 2y \end{pmatrix}
$$

Therefore

$$
J(0,0) = \begin{pmatrix} 0 & -1 \\ -1 & 0 \end{pmatrix}
$$

$\beta = 0, \gamma = -1$. So this is a saddle point.

$$
J(1,-1) = \begin{pmatrix} 2 & -1 \\ -1 & -2 \end{pmatrix}
$$

$\beta = 0, \gamma = -5$. So this is a saddle point.

$$
J(1,1) = \begin{pmatrix} 2 & -1 \\ -1 & 2 \end{pmatrix}
$$

$\beta = 4, \gamma = 3$. So this is an unstable node.
(f)

$$
\begin{aligned}
\frac{dx}{dt} &= -\frac{xy}{1+x} + x \\
\frac{dy}{dt} &= \frac{xy}{1+x} - y
\end{aligned}
$$

Steady states:

$$
\begin{aligned}
-\frac{xy}{1+x} + x &= 0 \\
\Longrightarrow x &= 0 \Longrightarrow y = 0 \\
\text{and} \Longrightarrow y &= x + 1 \text{ not possible}
\end{aligned}
$$

Steady state at $(0,0)$.
Jacobian:

$$
J(x,y) = \begin{pmatrix} \frac{-1}{(1+x)^2} + 1 & \frac{-x}{1+x} \\ \frac{1}{(1+x}^2 & \frac{x}{1+x} - 1 \end{pmatrix}
$$

Therefore

$$J(0,0) = \begin{pmatrix} 0 & 0 \\ 1 & -1 \end{pmatrix}$$

$\beta = -1, \gamma = 0$. So this is a stable node.
(g)

$$\begin{aligned} \frac{dx}{dt} &= xy(1-x) + C \\ \frac{dy}{dt} &= y(1 - \frac{y}{x}) \end{aligned}$$

Steady states:

$$\begin{aligned} y(1-\frac{y}{x}) &= 0 \\ \Longrightarrow y &= 0 \text{ or } y = x \end{aligned}$$

$y = 0$ would imply $C = 0$ and x arbitrary. $y = x$ implies $x^3 - x^2 = C$.
Jacobian:

$$J(x,y) = \begin{pmatrix} y - 2x & x \\ \frac{y^2}{x^2} & 1 - \frac{2y}{x} \end{pmatrix}$$

Therefore:

$$J(x,0) = \begin{pmatrix} -2x & x \\ 0 & 1 \end{pmatrix}$$

Thus $\beta = 1 - 2x$ and $\gamma = -2x$. If $x < 0$ this is an unstable node. If $x > 0$ this is a saddle.

$$J(x,x) = \begin{pmatrix} -x & x \\ 1 & -1 \end{pmatrix}$$

Thus $\beta = -x - 1$ and $\gamma = 0$, where x is the solution of $x^3 - x^2 = C$. For positive C, the only real solution to this equation is > 0, and hence the corresponding steady state is a stable node. For $C < -9/8$, the only solution is < 0. This solution is < 1, and hence the equilibrium is an unstable node, if $C < 2$, otherwise the steady state is a stable node. For $-9/8 < C < 0$, the equation has 3 solutions, which all correspond to $\beta < 0$, hence to a stable node.

3. (a) Nullclines at $y = 0$ and $x = 0$

$$J(x,y) = \begin{pmatrix} 0 & -2 \\ 1 & 0 \end{pmatrix}$$

So the steady state at $(0,0)$ is a centre.

(b) Nullclines at $y = -3/2x$ and $y = -4x$.

$$J(x,y) = \begin{pmatrix} 3 & 2 \\ 4 & 1 \end{pmatrix}$$

So steady state at $(0,0)$ is a saddle point.

(c) Nullclines at $y = -2x$ and $y = -1/2x$.

$$J(x,y) = \begin{pmatrix} 2 & 1 \\ 1 & 2 \end{pmatrix}$$

So steady state at $(0,0)$ is an unstable node.
(d) Nullclines at $y = -8/5x$, $y = -3/5x$

$$J(x,y) = \begin{pmatrix} 5 & 8 \\ -3 & -5 \end{pmatrix}$$

So steady state at $(0,0)$ is a saddle point.
(e) Note that there is a typo in the textbook. The first equation should read $dx/dt = -4x - 2y$ (otherwise $(0,0)$ would not be a steady state). Nullclines at $y = -2x$, $y = 3x$

$$J(x,y) = \begin{pmatrix} 4 & -2 \\ 3 & -1 \end{pmatrix}$$

So steady state at $(0,0)$ is a stable spiral.

(f) Nullclines at $y = 1/4x$, $y = -x$

$$J(x,y) = \begin{pmatrix} 1 & -4 \\ 1 & 1 \end{pmatrix}$$

So steady state at $(0,0)$ is an unstable spiral.

4.(a)

$$\begin{aligned}
\frac{dN_1}{dt} &= r_1 N_1 \left(\frac{K_1 - N_1 - \beta_{12}N_2 - \beta_{13}N_3 - \cdots - \beta_{1k}N_k}{K_1} \right) \\
\frac{dN_2}{dt} &= r_2 N_2 \left(\frac{K_2 - N_2 - \beta_{21}N_1 - \beta_{23}N_3 - \cdots - \beta_{2k}N_k}{K_2} \right) \\
&\vdots \\
\frac{dN_k}{dt} &= r_k N_k \left(\frac{K_k - N_k - \beta_{k1}N_1 - \beta_{k12}N_2 - \cdots - \beta_{kk-1}N_{k-1}}{K_k} \right)
\end{aligned}$$

(b) Number of steady states: 1 trivial solution; 3 with one species present and the other two absent; when only one species is absent, there are an additional 3 steady states with the other two species present; when all species are present there will be 1 steady state; this amounts to a total of 8.

(c) The steady state will be a stable spiral so that species will have oscillations which will be out of phase.

5. NOTE: the correct system of equations is as follows

$$\begin{aligned}\frac{dN_1}{dt} &= rN_1\left(1-\frac{N_1}{(K_1+\alpha N_2)}\right)\\ \frac{dN_2}{dt} &= rN_2\left(1-\frac{N_2}{(K_2+\beta N_1)}\right)\end{aligned}$$

(a) The carrying capacity is an increasing function of the size of the other population.

(b) Nullclines at $N_1 = 0$, $N_1 = K_1 + \alpha N_2$, $N_2 = 0$ and $N_2 = K_2 + \beta N_1$. We therefore have steady states at $(0,0)$, $(K_1, 0)$, $(0, K_2)$ and $\left(\frac{K_1+\alpha K_2}{1-\alpha\beta}, \frac{K_2+\beta K_1}{1-\alpha\beta}\right)$.

Computing the Jacobian:

$$J(x,y) = \begin{pmatrix} r\left(1-\frac{2N_1}{K_1+\alpha N_2}\right) & \frac{\alpha r N_1^2}{(K_1+\alpha N_2)^2} \\ \frac{\beta r N_2^2}{(K_2+\beta N_1)^2} & r\left(1-\frac{2N_2}{K_2+\beta N_1}\right) \end{pmatrix}$$

So

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

This is an unstable node.

$$J(K_1,0) = \begin{pmatrix} -r & \alpha r \\ 0 & r \end{pmatrix}$$

This is a saddle point.

$$J(0,K_2) = \begin{pmatrix} r & 0 \\ \beta r & -r \end{pmatrix}$$

This is a saddle point.

$$J\left(\frac{K_1+\alpha K_2}{1-\alpha\beta}, \frac{K_2+\beta K_1}{1-\alpha\beta}\right) = \begin{pmatrix} -r & \alpha r \\ \beta r & -r \end{pmatrix}$$

After looking at the trace and determinant we see that this is a stable node.

(c) $\alpha\beta < 1$ to ensure that there is steady state at which both species coexist at positive population sizes (i.e. such that $1 - \alpha\beta > 0$).

6. (a) If N is constant if and only if $\frac{dN}{dt} = 0$.

$$\begin{aligned}
\frac{dN}{dt} &= \frac{dS}{dt} + \frac{dI}{dt} + \frac{dR}{dt} \\
&= -\beta SI + \gamma R + \beta SI - \nu I + \nu I - \gamma R \\
&= 0
\end{aligned}$$

(b) Steady states:

$$\begin{aligned}
-\beta SI + \gamma R &= 0 \\
\beta SI - \nu I &= 0 \\
\nu I - \gamma R &= 0
\end{aligned}$$

From this we can see that $R = \frac{\nu I}{\gamma}$. Also

$$\begin{aligned}
I(\nu - \beta S) &= 0 \\
\implies S &= \frac{\nu}{\beta} \quad \text{or} \quad I = 0
\end{aligned}$$

If $I = 0$ then $R = 0$ so that $S = N$ (so that $\frac{dN}{dt} = 0$). If $S = \frac{\nu}{\beta}$ then

$$\begin{aligned}
I &= N - \frac{\nu}{\beta} - \frac{\nu I}{\gamma} \\
I\left(1 + \frac{\nu}{\gamma}\right) &= N - \frac{\nu}{\beta} \\
I &= \frac{\gamma}{\gamma + \nu}\left(N - \frac{\nu}{\beta}\right) \\
\implies R &= \frac{\nu}{\gamma + \nu}\left(N - \frac{\nu}{\beta}\right)
\end{aligned}$$

Thus there are steady states at $(S, I, R) = (N, 0, 0)$ and $(S, I, R) = \left(\frac{\nu}{\beta}, \frac{\gamma}{\gamma+\nu}\left(N - \frac{\nu}{\beta}\right), \frac{\nu}{\nu+\gamma}\left(N - \frac{\nu}{\beta}\right)\right)$.

(c) After adding birth and death rates, the equations become

$$\begin{aligned}
\frac{dS}{dt} &= -\beta SI + \gamma R + \delta N - \delta S \\
\frac{dI}{dt} &= \beta SI - \nu I - \delta I \\
\frac{dR}{dt} &= \nu I - \gamma R - \delta R
\end{aligned}$$

See figure 6.12(c) in the text book.

(d) Using the usual methods we find that there are two steady states of this system at $(S, I, R) = (N, 0, 0)$ as before and at $(S, I, R) = \left(\frac{\delta+\nu}{\beta}, \frac{1}{2}\left(N - \frac{\delta+\nu}{\beta}\right), \frac{\nu-\delta}{2\gamma}\left(N - \frac{\delta+\nu}{\beta}\right)\right)$.

The infectious contact number is $\frac{N\beta}{\delta+\nu}$.

(e) We compare the two models by looking at the stability of the two steady states.

1. The Jacobian for the first model is shown on page 248. The Jacobian for the model with vital dynamics added is

$$J(S, I) = \begin{pmatrix} -(\beta I + \gamma + \delta) & -(\beta S + \gamma) \\ \beta I & \beta S - (\nu + \delta) \end{pmatrix}$$

   Evaluating the two Jacobians at the steady states in the cases when the population is greater than or less than the infectious contact number reveals that the steady state $(S, I, R) = (0, 0, 0)$ is stable when the population is less than the contact number and a saddle point when the population is greater. The non zero steady state does not exist in this case. When the population is greater than the infectious contact number, the non trivial steady state is stable. This is true for both models. The difference between the two models lies in the critical population size needed to allow the disease to become endemic. In the case of the model with vital dynamics, this number is smaller since new susceptibles are generated by birth.

7. **Normal model** has steady states at $(0, 0)$ and $\left(\frac{c}{d}, \frac{a}{b}\right)$ which are a saddle point and a centre respectively.

With each of the following modifications, the stability of the steady states was checked by computing the trace and determinant of the Jacobian. In each case the Jacobian is given, then the steady states are listed with either the trace and determinant of the Jacobian evaluated at the steady state or the eigenvalues and the conclusion of the stability analysis.

Pielou's modification:
This adds logistic growth to the prey population model. See problem 8 for details.

Rosenzweig's modification:
This model penalizes low population levels. If $x < K$ then the population growth rate will be negative. If $x > K$ then the growth rate is positive and

increases with increasing x so growth is similar to exponential growth. The Jacobian is given by:

$$J(x,y) = \begin{pmatrix} r(g+1)\left(\frac{K}{x}\right)^{-g} - r - by & -bx \\ dy & dx - c \end{pmatrix}$$

This again has three steady states: $(0,0)$ is stable $(\lambda_{1,2} = -r, -c)$,$(K,0)$ is unstable $(\lambda_{1,2} = rg, dK - c)$ and $\left(\frac{c}{d}, \frac{r}{b}\left(\left(\frac{kD}{c}\right)^{-g} - 1\right)\right)$ is also unstable ($\beta = gr\left(\frac{Kd}{c}\right)^{-g} > 0$ and $\gamma = rc\left(\left(\frac{Kd}{c}\right)^{-g} - 1\right) > 0$).

Schoener's modification:
If $x < K$ then the population growth rate is positive. However if $x > K$ then the growth rate is negative and the population will try to return to K. Jacobian:

$$J(x,y) = \begin{pmatrix} -r - by & -bx \\ dy & dx - c \end{pmatrix}$$

Again three steady states at $(0,0)$ (eigenvalues as for other models - stable), $(K,0)$ (eigenvalues as for other models - saddle) and $\left(\frac{c}{d}, \frac{r}{b}\left(\frac{Kd}{c} - 1\right)\right)$. $\beta = -\frac{rKd}{c}$ and $\gamma = cr\left(\frac{Kd}{c} - 1\right)$. This is stable.

Modification of attack rates:

Ivlev:
This modification of the attack rate maximizes it at the number of predators. At low prey numbers though there are more attacks when compared to the simple model. The Jacobian for the system is:

$$J(x,y) = \begin{pmatrix} a - ckye^{-cx} & -k(1 - e^{-cx}) \\ dy & dx - c \end{pmatrix}$$

The result is two steady states at $(0,0)$ (eigenvalues $= a, -c$ - (saddle) and $\left(\frac{c}{d}, \frac{ac}{kd\left(1 - e^{-\frac{c^2}{d}}\right)}\right)$. Looking at the trace and determinant shows that this is stable.

Holling:
This adds a sort of carrying capacity to the attack rate. The Jacobian is:

$$J(x,y) = \begin{pmatrix} a - \frac{kDy}{(x+D)^2} & \frac{kx}{x+D} \\ dy & dx - c \end{pmatrix}$$

The trivial steady state is once again a saddle while the other steady state at $\left(\frac{c}{d}, \frac{a}{k}\left(\frac{c}{d} + D\right)\right)$ is unstable ($\beta = \frac{ac}{d\left(\frac{c}{d} + D\right)}$, $\gamma = ac$.)

Rosenzweig:
This is very similar to the original except that it place less importance on the number of prey present.

$$J(x,y) = \begin{pmatrix} a - gkyx^{g-1} & kx^g \\ dy & dx - c \end{pmatrix}$$

The trivial steady state is a saddle while $\left(\frac{c}{d}, \frac{a}{k}\left(\frac{d}{c}\right)^{g-1}\right)$ is stable ($\beta = a(1-g)$, $\gamma = ac$).

Finally **Takahashi's modification** is similar to Hollings.

$$J(x,y) = \begin{pmatrix} a - \frac{2kxyD^2}{(x^2+D^2)^2} & \frac{kx^2}{x^2+D^2} \\ dy & dx - c \end{pmatrix}$$

Trivial steady state is still a saddle while the non trivial steady state at $\left(\frac{c}{d}, \frac{ad}{kc}\left(\left(\frac{c}{d}\right)^2 + D^2\right)\right)$ is stable as long as $\frac{c}{d} > D$ ($\gamma = \frac{a}{\left(\frac{c}{d}\right)^2 + D^2}\left(\frac{c}{d}\right)^2 - D^2$, $\beta = ac$).

8. From the Jacobian (shown on pg 222), $\beta = -\frac{ac}{dK}$ and $\gamma = bc\left(\frac{a}{b} - \frac{ac}{dbK}\right)$. This is stable, because we need $1 > c/(dK)$ for the steady state level of the predator to be positive., so that $\gamma > 0$. To see whether this is a stable node or a stable focus, we calculate:

$$\begin{aligned} \beta^2 - 4\gamma &= \frac{(ac)^2}{(dK)^2} - 4bc\left(\frac{a}{b} - \frac{ac}{dbK}\right) \\ &= \frac{ac}{(dK)^2}\left(ac - 4(dK)^2 + 4cdK\right) \end{aligned}$$

The sign of this expression is determined by the sign of $ac - 4(dK)^2 + 4cdK = ac - 4(dK)^2\,(1 - c/(dK))$. Thus, if

$$ac < 4(dK)^2\,(1 - c/(dK))$$

then the equilibrium is a stable focus, otherwise it is a stable node.

9. Nullclines for this model:
x nullclines: $x = 0$, $y = \frac{r}{a}\left(1 - \frac{x}{K}\right)$,
y nullclines: $y = 0$, $y = bx$.

Thus there are steady states at $(K, 0)$ and $\left(\frac{rK}{abK+r}, \frac{rbK}{abK+r}\right)$. Note that $(0,0)$ is not a steady state since $x \neq 0$.

The Jacobian for this system is given below:

$$J(x,y) = \begin{pmatrix} r - \frac{2rx}{K} - ay & -ax \\ \frac{sy^2}{bx^2} & s - \frac{2sy}{bx} \end{pmatrix}$$

Evaluating this at the steady state:

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

So this is a saddle point.

$$J\left(\frac{rK}{abK+r}, \frac{rbK}{abK+r}\right) = \begin{pmatrix} -\frac{r^2}{abK+r} & -\frac{arK}{abK+r} \\ bs & -s \end{pmatrix}$$

This is a stable node, because $tr(J) < 0$ and $\det(J) > 0$.

10. A simple curve means, intuitively speaking, a curve which does not intersect itself. For example, Figure 8.1(a) represents a simple curve, but Figure 8.1(b) does not and can therefore not be the solution to a differential equation. Specifically, for the coordinates at the intersection point the two functions describing the rates of change in x and y would have to multi-valued, i.e. not well defined. Also, Figure 8.1(c) cannot be a limit cycle since when a trajectory arrives at the steady state (indicated by the dot) it will remain there (since $dx/dt = 0$ and $dy/dt = 0$ at the steady state) and so there can be no circulation around the path.

11. (a) First equation:
First term: prey growth rate, with a quadratic function of the per capita growth rate, which implies that the per capita growth is small at low prey population densities (e.g. due to an Allee effect), then increases with prey population size, and finally decreases again with prey population size to negative values for prey population sizes that are > 1.
Second term: attack rate
Second equation:
First term: attack rate
Second term: prey death rate.

(b) x nullclines: $x = 0$, $y = x(1-x)$
y nullclines: $y = 0$, $x = \frac{1}{\mu}$. Cannot apply Poincaré-Bendixson theorem (look at large y). See p. 565 in the textbook.

(c) Looking at the intersection of the nullclines we see that there are steady states at $(0,0)$, $(1,0)$ and $\left(\frac{1}{\mu}, \frac{1}{\mu}\left(1 - \frac{1}{\mu}\right)\right)$.

(d) The Jacobian for the system is

$$J(x,y) = \begin{pmatrix} 2x - 3x^2 - y & -x \\ ky & k\left(x - \frac{1}{\mu}\right) \end{pmatrix}$$

$$J\left(\frac{1}{\mu}, \frac{1}{\mu}\left(1 - \frac{1}{\mu}\right)\right) = \begin{pmatrix} \frac{1}{\mu} - \frac{2}{\mu^2} & -\frac{1}{\mu} \\ \frac{k}{\mu}\left(1 - \frac{1}{\mu}\right) & 0 \end{pmatrix}$$

(e) Looking at the trace and determinant of the Jacobian matrix, we see that $tr(J) = \frac{1}{\mu} - \frac{2}{\mu^2}$ only depends on μ, which is therefore the bifurcation parameter. $tr(J) = 0$ occurs for $\mu = 2$, with $tr(J) < 0$ for $\mu < 2$. Now, for $\mu = 2$ we have $Det(J) = k/4 - k/8 > 0$, hence a Hopf bifurcation occurs at $\mu = 2$, with the equilibrium being a stable focus for $\mu < 2$ and an unstable focus for $\mu > 2$.

12. (a) There are always steady states at $x = 0$ and $x = 1$. The shape of the function $f(x,y) = x(1-x)(\alpha(1-y) + x)$, and hence the dynamics of x for a given value of y, depends on the value of the term $\alpha(1-y)$. If this term is > 0 then the function will be > 0 for $0 < x < 1$ and hence x will converge to 1. If $-1 < \alpha(1-y) < 0$ then $f(x,y) < 0$ for $0 < x < -\alpha(1-y)$ and $f(x,y) > 0$ for $-\alpha(1-y) < x < 1$. Therefore, plant quality will converge towards 0 or 1 depending on whether $x(0)$ is bigger or smaller than $-\alpha(1-y)$. If $\alpha(1-y) < -1$, then $f(x,y) < 0$ for $0 < x < 1$, hence plant quality will converge towards 0.

(b)

$$g(x,y) = \beta(1 - \frac{y}{Kx})$$

(c) If the steady state at $\left(\frac{\alpha}{K\alpha-1}, \frac{K\alpha}{K\alpha-1}\right)$ is in the positive quadrant, then the two isoclines intersect in such a way that there is region around the steady state that traps the flow.

(d) Looking at the intersection of nullclines we see that there are other steady states at $(1,0)$ and $(1,K)$.

$$J(x,y) = \begin{pmatrix} 2(1-\alpha)x + \alpha(1-y) + 2\alpha xy - 3x^2 & -\alpha x(1-x) \\ \frac{\beta y^2}{Kx^2} & \beta\left(1 - \frac{2y}{Kx}\right) \end{pmatrix}$$

Evaluating the Jacobian at the steady state $(\gamma, K\gamma)$, where $\gamma = \frac{\alpha}{K\alpha-1}$, we find that the determinant $\det(J) = \frac{\alpha\beta(\alpha K - 1 - \alpha)}{\alpha K - 1}$. Thus if $\gamma > 1$, hence if $\alpha > \alpha K - 1$, this determinant will be negative, in which case the steady state is a saddle point. If $\gamma < 1$, the determinant will be positive.

(e) The trace of the Jacobian at the steady state $(\gamma, K\gamma)$ is $tr(J) = \frac{\alpha}{(\alpha K-1)^2}(\alpha K - 1 - \alpha) - \beta$. If $\gamma < 1$, hence if $\alpha < \alpha K - 1$, then the first term in the formula for the trace is positive. Therefore, the trace will be negative for large values of β and will become negative for small β. Since the determinant remains positive, this means that we see a Hopf bifurcation as β is decreased from large to small values.

(f) Combining the Hopf bifurcation theorem with the existence of a trapping region around the steady state (see (c) above), we conclude that there is a stable limit cycle for a range of small β values. (From the Hopf bifurcation theorem we know that there exists a unique periodic solution for a range of β values that lie either above or below the bifurcation point. But below the bifurcation point, we know that the steady state is an unstable focus, and we know that there is a trapping region, hence we conclude from Poincaré-Bendixson theory that there is a limit cycle. Therefore, we must be in the situation where the limit cycles from the Hopf bifurcation theorem occur for a range of β values below the bifurcation point, for which the steady state is unstable, and the limit cycle is stable according to the Poincaré-Bendixson theorem, because it is unique according to the Hopf bifurcation theorem.)

As the reproductive rate of the herbivores decreases, the steady state that is achieved becomes unstable and is replaced by oscillations in the number of herbivores and plant quality. At some stage, the number of herbivores is low enough that it allows for an improvement in the plant quality. This in turn allows for an increase in the number of herbivores, decreasing the plant quality, again reducing the number of herbivores. This cycle repeats itself.