MATH3070
Natural Resource Mathematics
Lecture Notes: Two Dimensional Models in Natural Resource Mathematics

These notes are Matthew Holden's summary of selected sections from
C.W. Clark., *"Mathematical Biometrics: The Mathematics of Conservation"*, 3rd ed.,
Wiley, 2010. Along with some additional content.

1 Multi-Species Models

The previous analysis for a single species can be extended to several species. In what follows, we will focus on the extension to two-species. A general two-species model with species x and y could be of the form

$$x_1' = G_1(x_1, x_2) - H_1(x_1)$$
$$x_2' = G_2(x_1, x_2) - H_2(x_2),$$

where G_i and H_i are the growth and harvest functions of species i for $i \in \{1, 2\}$. Following Schaefer's assumption, that harvest is proportional to abundance, we would consider

$$x_1' = G_1(x_1, x_2) - q_1 E_1 x_1,$$
$$x_2' = G_2(x_1, x_2) - q_2 E_2 x_2,$$

(1)

where q_1 and q_2 are the catchability factors of species one and two, respectively. Harvest effort for species one is E_1 and E_2 is the effort of harvest for species two.

Dependent on the functional forms of G_1 and G_2, species one and two can be competitors, mutualists, or be in a predator-prey relation.

- If $\frac{\partial G_1(x_1, x_2)}{\partial x_2}, \frac{\partial G_2(x_1, x_2)}{\partial x_1} > 0$, then the species are having a mutualistic relation.

- If $\frac{\partial G_1(x_1, x_2)}{\partial x_2} > 0$, and $\frac{\partial G_2(x_1, x_2)}{\partial x_1} < 0$, then the species are in a predator-prey relation, where species one is the predator and species two is the pray.

- If If $\frac{\partial G_1(x_1, x_2)}{\partial x_2}, \frac{\partial G_2(x_1, x_2)}{\partial x_1} < 0$, then the species are competitors.

One should note that there can be combinations of these base forms, as species in a mutualism could become competitors after a certain density dependent threshold is reached.

While the functions G and H determine the biological dependence of species, the harvest terms reveal their economic relation. For example, if both species, independent of their biological relation, are being harvested with the same method, then $E_1 = E_2$ and the species are linked economically.

Questions of interest when investigating (1) are similar to one-species models you discussed earlier and cover the stability of a equilibria, the existence of a "bionomic equilibrium", as well as the optimal harvest policies. Let us address these questions in the following, starting with the stability of the biologic equilibrium.

1.1 Biological Equilibrium

To determine the biological equilibrium of (1), we find all pairs (x^*, y^*) such that

$$x_1'(x_1^*, x_2^*) = 0 \qquad \Leftrightarrow \qquad G_1(x_1^*, x_2^*) = q_1 E_1 x_1^*,$$
$$x_2'(x_1^*, x_2^*) = 0 \qquad \Leftrightarrow \qquad G_2(x_1^*, x_2^*) = q_2 E_2 x_2^*.$$

Once these pairs are obtained, we have found the biological equilibria of (1). As some of these euqilibria might be undesirable from a ecological perspective, we are interested in further determining the stability of these equilibria. For that, we use the following Theorem from the *Theory of Differential Equations*.

Consider
$$\mathbf{x}' = f(\mathbf{x}) = A(\mathbf{x} - \mathbf{x}^*) + g(\mathbf{x}), \tag{2}$$

where $\mathbf{x}^* \in \mathbb{R}^n$ is an equilibrium and $A \in \mathbb{R}^{n \times n}$ is the Jacobian of $f = (f_1, f_2, \ldots, f_n)$ evaluated at the equilibrium $\mathbf{x}^*$, often denoted by $J_{\mathbf{x}^*}$, that is

$$J_{\mathbf{x}^*} = A = \begin{bmatrix} \frac{\partial f_1(\mathbf{x}^*)}{\partial x_1} & \frac{\partial f_1(\mathbf{x}^*)}{\partial x_2} & \cdots & \frac{\partial f_1(\mathbf{x}^*)}{\partial x_n} \\ \frac{\partial f_2(\mathbf{x}^*)}{\partial x_1} & \frac{\partial f_2(\mathbf{x}^*)}{\partial x_2} & \cdots & \frac{\partial f_2(\mathbf{x}^*)}{\partial x_n} \\ \vdots & \vdots & \cdots & \vdots \\ \frac{\partial f_n(\mathbf{x}^*)}{\partial x_1} & \frac{\partial f_n(\mathbf{x}^*)}{\partial x_2} & \cdots & \frac{\partial f_n(\mathbf{x}^*)}{\partial x_n} \end{bmatrix}$$

and let $g = (g_1, g_2, \ldots, g_n)$ satisfy

$$\lim_{\mathbf{x} \to \mathbf{x}^*} \frac{\|g(\mathbf{x})\|}{\|\mathbf{x} - \mathbf{x}^*\|} = 0. \tag{3}$$

Theorem 1 *[See Theorem 3.26 in "Theory of Differential Equations" by Kelley and Peterson] Consider (2) and assume (3), then the following holds:*

- *If all eigenvalues of A have negative real parts, then the equilibrium $\mathbf{x}^*$ is (locally) asymptotically stable.*

- *If at least one eigenvalue of A has a positive real part, then the equilibrium $\mathbf{x}^*$ is unstable.*

It is worth mentioning that the same authors have a book on discrete mathematics, in which they present a discrete analogue of Theorem 1 [See Corollary 4.3 in "Difference Equations" by Kelley and Peterson]. The Theorem reads then as follows: If $\mathbf{x}^*$ is a fixed point of $x_{t+1} = f(x_t)$ and all eigenvalues of the Jacobian of f evaluated at $\mathbf{x}^*$ are in absolute value less than one, then the equilibrium is (locally) asymptotically stable.

Recall some vocabulary for a 2-dimensional (continuous) system:

- An equilibrium, x^* is called **asymptotically stable** if for every $\epsilon > 0$, there exists $\delta_1 > 0$, such that if $||x(0) - x^*|| < \delta_1$, then for all $t \geq 0$, $||x(t) - x^*|| < \epsilon$. Additionally, there exists $\delta_2 > 0$, such that if $||x(0) - x^*|| < \delta_2$, $\lim_{x \to \infty} ||x(t) - x^*|| = 0$.

- If the eigenvalues are real and negative, the equilibrium is called a **sink node** (stable).

- If the eigenvalues are real and positive, the equilibrium is called a **source node** (unstable).

- If the eigenvalues are real, one is positive and one is negative, the equilibrium is called a **saddle point** (unstable).

- If the eigenvalues are complex conjugates with negative real parts, the equilibrium is called a **spiral sink** (stable).

- If the eigenvalues are complex conjugates with positive real parts, the equilibrium is called a **spiral source** (unstable).

- If both equilibria are purely imaginary, the equilibrium of the linear system is a **centre**. Note centre's are borderline cases, where the nonlinear system is not guaranteed to behave like the linear system. In this case, further investigation is needed to make rigorous statements about the dynamics. **Question:** Why is this consistent with Theorem 1?

Example Multi-Species Harvest Model:

Let us consider the following 2-species model :

$$x_1' = r_1 x_1 \left(1 - \frac{x_1}{k}\right) - a x_1 x_2 - q_1 E_1 x_1, \tag{4}$$

$$x_2' = b a x_1 x_2 - m x_2 - q_2 E_2 x_2, \tag{5}$$

with all parameters strictly positive. In what type of relation are the two species in?

1.2 Non-dimensionalisation

This model will be much easier to understand if we simplify the notation. To do this we must study the theory of Dimensional Analysis. That is because, to simplify the notation, we will need to "non-dimensionalize" the system. This is important for two reasons: (1) it allows us to reduce the number of parameters and (2) it allows researchers to study the qualitative features of the model without having to worry if their model is using the same units as another model (in other words it makes the results from various models comparable to each other). The goal is to write an equivalent system, in terms of new, rescaled state variables and parameters that are unitless. It is easiest to show the power of nondimensionalisation, by going through an example (we will choose the predator-prey model above). In mathematical physics there is a theorem called the **Buckingham π Theorem** that makes nondimensionalisation more mathematically rigorous. It takes more than two pages to state formally, and requires a lot of new notation and definitions, so we will not go over it in detail here. However, the informal version, effectively says that if there is a physically meaningful equation with n variables, then the original equation can be rewritten using $n-l$ dimensionless parameters $\pi_1, \pi_2, ..., \pi_{n-l}$ constructed from the original variables, where l is the number of physical dimensions obtained as the rank of a dimensional matrix. For more details see the first chapter of G.W. Bulman and S. Kumei, "Symmetries and Differential Equations", Springer-Verlag, 2013, which includes a formal statement and proof of the theorem.

We start our nondimensionalisation of the system specified by equations (4) and (5) by introducing the new state variables,

It is useful to write the original system as

$$\frac{dx_1}{dt} = (r_1 - q_1 E_1)x_1 - \frac{r x_1^2}{k} - a x_1 x_2, \qquad (6)$$

$$\frac{dx_2}{dt} = b a x_1 x_2 - (m + q_2 E_2)x_2, \qquad (7)$$

Then we note that

Our goal is to choose the constants that re-scale the state variables in a way that eliminates as many parameters as possible. Looking at the above system I can choose,

I can also define new parameters,

with the above specified variables and parameters, the new system of equations is,

we have amazingly reduced the system to only two parameters! This will make studying the system so much easier. Note other choices for x and y are possible. For example, one might choose $x = x_1/k$ as the rescaled state variable for species one. This is a natural choice, because it makes x quite easy to interpret biologically. However, this rescaling leaves us with three parameters instead of two. Often there is a trade-off between different choices of the constants used to nondimensionalise the system. It is up to the modeller to choose the one that is best for the particular problem they are trying to solve. Now that we have nondimensionalised the system we are ready to analyse it.

1.3 Qualitative behaviour of the multi-species harvest model

The new system is

$$\frac{dx}{d\tau} = \rho x - \mu x^2 - xy, \tag{8}$$

$$\frac{dy}{d\tau} = xy - y. \tag{9}$$

To calculate the possible equilibria, we set the above equal to zero, and solve for x and y to obtain

$$(0,0), \quad \left(\frac{\rho}{\mu}, 0\right), \quad (1, \rho - \mu),$$

Note that $\left(\frac{\rho}{\mu}, 0\right)$ is only biologically relevant if $\rho > 0$, as $\mu := \frac{r}{kba}$ is always positive. Recall that $\rho = (r - q_1 E_1)/(m + q_2 E_2)$, and hence this equilibrium is positive if $r > q_1 E_1$. Similarly, $(1, \rho - \mu)$ is only biologically relevant if $\rho > \mu$. To discuss the stability, we obtain the Jacobian J by realizing that

$$f_1 = \rho x - \mu x^2 - xy$$
$$f_2 = xy - y$$

Hence, the Jacobian is

$$J(x, y) = \begin{bmatrix} \rho - 2\mu x - y & -x \\ y & x - 1 \end{bmatrix}. \tag{10}$$

We can immediately see that

$$J(0, 0) = \begin{bmatrix} \rho & 0 \\ 0 & -1 \end{bmatrix}.$$

Recall that $\rho = (r - q_1 E_1)/(m + q_2 E_2)$. So this equilibrium has only negative eigenvalues if $r < q_1 E_1$. Hence, by Theorem 1, the trivial equilibrium, $(0,0)$, is locally stable in this case. If $r > q_1 E_1$, then the trivial equilibrium is an unstable saddle. (**Note:** If equality holds, then we have to use other tools to discuss the stability). **Question:** Why does this condition for the stability of $(0,0)$ make sense biologically?

Similarly, the Jacobian evaluated at $\left(\frac{\rho}{\mu}, 0\right)$ is

$$J\left(\frac{\rho}{\mu}, 0\right) = \begin{bmatrix} -\rho & -\frac{\rho}{\mu} \\ 0 & \frac{\rho}{\mu} - 1 \end{bmatrix},$$

which has the eigenvalues $-\rho$, and $\frac{\rho}{\mu} - 1$.

The Jacobian evaluated at $(1, \rho - \mu)$ is

$$J(1, \rho - \mu) = \begin{bmatrix} -\mu & -1 \\ \rho - \mu & 0 \end{bmatrix},$$

So

$$\det \begin{bmatrix} -\mu - \lambda & -1 \\ \rho - \mu & -\lambda \end{bmatrix} = 0,$$

which yields the characteristic equation

$$\lambda^2 + \mu\lambda + \rho - \mu = 0,$$

which has solutions

$$\lambda = \frac{-\mu \pm \sqrt{\mu^2 - 4(\rho - \mu)}}{2}$$

.

Note that if the $4(\rho - \mu) < 0$ or equivalently $\rho < \mu$, we would have one positive and one negative eigenvalue, an unstable saddle. **Question:** Is this possible?

If the $\mu^2 - 4(\rho - \mu) < 0$, the eigenvalues are complex with a negative real part (stable spiral). The condition simplifies to $\rho > \frac{\mu^2}{4} + \mu$. If $\mu < \rho < \frac{\mu^2}{4} + \mu$, then both eigenvalues are negative, meaning the equilibrium is a stable node.

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Sketch the qualitative trajectories in phase space for $\rho < 0$

Sketch the qualitative trajectories in phase space for $0 < \rho < \mu$

Sketch the qualitative trajectories in phase space for $\mu < \rho < \frac{\mu^2}{4} + \mu$

Sketch the qualitative trajectories in phase space for $\rho > \frac{\mu^2}{4} + \mu$

1.4   Maximum Sustainable Yield

Similar to single population models, one can maximize the optimal harvest policy under sustainable conditions, that is, considering the model to be at the coexistence equilibrium.

The general approach to obtain the <u>Maximum Sustainable Yield</u> or, in that regard, the <u>Optimal Effort Level</u> that results in the maximum sustainable yield, contains of the following steps:

1. Obtain the co-existing equilibrium (make sure it is stable) dependent on effort E.

2. Set up the catch function at this equilibrium as a function of E.

3. Maximize the catch with respect to E.

Example:
Consider system (6). We wish to determine the maximum sustainable yield, where both the predator and prey coexist, if possible. Yield is given by

$$Y(E_1, E_2) = q_1 E_1 x_1 + q_2 E_2 x_2.$$

The coexistence equilibrium of the rescaled system is $(1, \rho - \mu)$, which corresponds to

$$x_1 = \frac{m + q_2 E_2}{ba}$$
$$x_2 = \frac{(m + q_2 E_2)(\rho - \mu)}{a} = \frac{abk(r - q_1 E_1) - (m + q_2 E_2)}{a^2 bk}.$$

So, with some algebra, the yield, at the co-existence equilibrium, is then given by

$$Y(E_1, E_2) = \left(\frac{mq_1}{ab}\right)E_1 + \left(\frac{q_1q_2}{a}\right)\left(\frac{1-b}{b}\right)E_1E_2 + \frac{rq_2}{a}\left(1 - \frac{m}{kba}\right)E_2 - \left(\frac{q_2^2 r}{kba^2}\right)E_2^2,$$

which we aim to maximize with respect to E_1, and E_2. When maximizing a function of two variables, we first obtain the critical values, that is E_1^c, E_2^c such that

$$0 = \frac{\partial Y}{\partial E_1}(E_1^c, E_2^c) = \frac{q_1(m - (b-1)E_2q_2)}{ab}$$

$$0 = \frac{\partial Y}{\partial E_2}(E_1^c, E_2^c) = \left(\frac{q_1q_2}{a}\right)\left(\frac{1-b}{b}\right)E_1^c + \frac{rq_2}{a}\left(1 - \frac{m}{kba}\right) - 2\left(\frac{q_2^2 r}{kba^2}\right)E_2^c$$

which yields

$$E_2^c = \frac{m}{q_2(b-1)}$$

$$E_2^c = \frac{r(ab^2k - abk - m - bm)}{akq_1(b-1)^2}.$$

Once the critical values (E_1^c, E_2^c) are obtained, we need to make sure it is a maximum. For that, we need

$$\frac{\partial^2 Y(E_1^c, E_2^c)}{\partial E_1^2} < 0$$

$$\frac{\partial^2 Y(E_1^c, E_2^c)}{\partial E_1^2}\frac{\partial^2 Y(E_1^c, E_2^c)}{\partial E_2^2} - \frac{\partial^2 Y(E_1^c, E_2^c)}{\partial E_1 \partial E_2} > 0.$$

The above is the second derivative test from multivariable calculus, using the Hessian matrix. We note that in our case,

$$\frac{\partial^2 Y(E_1^c, E_2^c)}{\partial E_1^2} = 0.$$

So the above critical value is not a maximum! It is, in fact, a saddle. So how do we find the maximum if the critical point is not the maximum?

There are a couple of ways to do this. But the key is you have to check the boundary of the region one is maximizing over (just like the end-points back in one dimensional models). Note we have as a condition for the co-existence equilibrium to exist, $\rho > \mu$. This coexistence condition, can be rewritten as

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$$E_1 < \frac{r}{q_1}\left(1 - \frac{E_2 q_2 + m}{abk}\right) \tag{11}$$

So the boundary is the union of these three line segments

$$L_1 := \left\{ (E_1, 0) : 0 \le E_1 < \frac{r}{q_1}\left(1 - \frac{m}{abk}\right) \right\}$$

$$L_2 := \left\{ (0, E_2) : 0 \le E_2 < \frac{abk + m}{q_2} \right\}$$

$$L_3 := \left\{ (E_1, E_2) : E_1 = \frac{r}{q_1}\left(1 - \frac{m}{abk}\right), E_1 > 0, E_2 > 0 \right\}$$

One way to approach this optimization problem is to use the KKT conditions, another way is to solve the problem over each segment of the boundary separately. Then compare the yield over those 3 solutions. If $E_2 = 0$, then

$$\frac{\partial Y}{\partial E_1} = \frac{mq_1}{ab},$$

Which means the optimal effort for species one is as high as possible, until E_1 reaches the constraint (e.g. the end of the line segment $L1$).

Question: What happens at this constraint? Which species goes extinct?

If $E_1 = 0$ then

$$\frac{\partial Y}{\partial E_2} = \frac{rq_2}{a}\left(1 - \frac{m}{kba}\right) - 2\left(\frac{q_2^2 r}{kba^2}\right)E_2$$

Setting this quantity equal to zero, and solving for E_2 yields,

$$E_2 = \frac{abk - m}{2q_2}.$$

We can verify this is indeed a local maximum by noting

$$\frac{\partial^2 Y}{\partial E_2^2} = -2\left(\frac{q_2^2 r}{kba^2}\right),$$

which is always negative. So the above fishing effort is optimal if only fishing the predator (e.g. its the optimal effort over the line segment $L2$).

If on segment L_3, of the boundary, we can use Lagrange multipliers to solve for the local optima. Let

$$g(E_1, E_2) = E_1 - \frac{r}{q_1}\left(1 - \frac{E_2 q_2 + m}{abk}\right)$$

Then we define the Lagrangian,

$$\mathcal{L}(E_1, E_2) = Y(E_1, E_2) - \lambda g(E_1, E_2)$$

And perform our optimisation. If we do this we get

$$E_1 = \frac{r}{2q_1} \tag{12}$$

and

$$E_2 = \frac{2m - abk}{2q_2}. \tag{13}$$

We can see, by plugging in (13) into (11), and comparing with (12), that this solution lies exactly on the extinction threshold for species two, the predator. So, technically to meet the co-existence constraint you would want to harvest ϵ below this level where ϵ is infinitesimally close to zero.

So now we need only compare the three solutions. Note the first solution, fishing at maximum effort on species one is also on the the line segment L_3 and is therefore dominated by the the solution above. So we need only compare the solution to the $\left(0, \frac{abk-m}{2q_2}\right)$ case.

$$Y\left(0, \frac{abk - m}{2q_2}\right) = \frac{r(m - abk)^2}{4a^2bk}$$

$$Y\left(\frac{r}{2q_1}, \frac{2m - abk}{2q_2}\right) = \frac{rk}{4}$$

So it is optimal to harvest only the predator species if

$$\frac{r(m - abk)^2}{4a^2bk} > \frac{rk}{4}$$

One can now show by equating these two quantities and solving for m there is that there are two roots $m = ak(b \pm \sqrt{b})$. The root with the plus is greater than abk and we already know there is no coexistence in that case. The interesting root is $m = ak(b - \sqrt{b})$. It is clear that this is negative if $b < 1$. So the root is only positive for $b > 1$. When $b > 1$ though, the left hand side will be small for values of m close to abk meaning the left hand side will be larger (i.e. want to only harvest the predator) if m is smaller than this root.

Figure 1: Bifurcation diagram for MSY

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Figure 2: Yield vs. E_1 and E_2 if $r = m = 3, q_1 = q_2 = 1, k = 100$ and $b = 0.5$
`Fig_m_b_bif_diagram_Pred_Prey_Harv_MSY.pdf`

The full story:

- If $m > abk$ no co-existence possible, even without harvest

- If $\frac{abk}{2} < m < abk$ it is optimal to harvest the prey exclusively, at rate $E_1 = r/(2q_1)$, and the predator naturally goes extinct `Yield_vs_E1_E2_low_m_b.pdf`

- If $ak(b - \sqrt{b}) < m < \frac{abk}{2}$. It is optimal to harvest the predator at high enough effort so that it goes extinct, and harvest the prey at effort $E_1 = r/(2q_1)$

- If $m < ak(b - \sqrt{b})$. It is optimal to harvest the predator only, at rate $E_2 = \frac{abk - m}{2q_2}$

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Figure 3: Yield vs. E_1 and E_2 if $r = m = 3, q_1 = q_2 = 1, k = 100$ and $b = 2$