Evolutionary Dynamics Homework 7

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Problem 1: Lotka-Volterra equation

The Lotka-Volterra equation is a famous example of theoretical ecology. Originally, it describes the dynamics of prey fish and predators. Let x denote the abundance of prey and y the number of predators. The dynamics is then given by

$$\begin{aligned} \dot{x} &= x(a - by) \\ \dot{y} &= y(-c + dx) \end{aligned} \tag{1}$$

with positive coefficients a, b, c, and d.

(a) What are the fixed points (x^*, y^*) of this system?

The fixed points are the solutions to the following equations:

$$\begin{aligned} 0 &= x(a - by) \\ 0 &= y(-c + dx) \end{aligned}$$

It's clear that we have solutions:

$$\begin{cases} x^* = 0 \\ y^* = 0 \end{cases}, \quad \text{and} \quad \begin{cases} x^* = c/d \\ y^* = a/b \end{cases}$$

(b) Use a linear stability analysis to determine the nature of the non-trivial fixed point. Describe the resulting dynamics qualitatively.

Hint: Consider the following steps:

Calculate the Jacobian of the right-hand-side of (1) and evaluate your expression at the fixed point (x^*, y^*). Then compute its eigenvalues. The real part of the eigenvalues determines whether the fixed point is attractive, whereas the imaginary part indicates oscillatory behaviour.

Compute the eigenvalues of the Jacobian at the non-trivial fixed point.

The Jacobian of the RHS of (1) is:

$$J = \begin{bmatrix} a - by & -bx \\ dy & -c + dx \end{bmatrix}$$

Evaluate at the non-trivial fixed point $(x^*, y^*) = (c/d, a/b)$:

$$\begin{aligned} J^* &= \begin{bmatrix} a - by^* & -bx^* \\ dy^* & -c + dx^* \end{bmatrix} \\ &= \begin{bmatrix} 0 & -bc/d \\ ad/b & 0 \end{bmatrix} \end{aligned}$$

The eigenvalues of J^* can be calculated as:

$$\begin{aligned} \det(J^* - \lambda I) &= \det \begin{bmatrix} -\lambda & -bc/d \\ ad/b & -\lambda \end{bmatrix} \implies \begin{cases} \lambda_1 = i\sqrt{ac} \\ \lambda_2 = -i\sqrt{ac} \end{cases} \\ &= \lambda^2 + ac \end{aligned}$$

Analyze the stability of the non-trivial fixed point.

The eigenvalues both have a zero real part, indicating that the equilibrium is *neither attractive nor repulsive*. The non-zero imaginary part indicates that the equilibrium is oscillatory with a period of $\sqrt{ac}$.

(c) Now consider the general Lotka-Volterra equation for n species y_i with real coefficients r_i, b_{ij}. Show that (2) can be derived from a replicator equation with $n+1$ strategies x_i.

$$\dot{y_i} = y_i \left(r_i + \sum_{j=1}^{n} b_{ij} y_j \right) \tag{2}$$

The replicator equation with $n+1$ strategies (from the slides):

$$\begin{aligned} \dot{x_i} = x_i[f_i(x) - \phi(x)], \quad & i = 1, \dots, n+1 \\ & x_1 + \cdots + x_{n+1} = 1 \end{aligned}$$

Consider payoff matrix $A = (a_{ij})$, $f_i(x)$ is the fitness of strategy i and $\phi(x)$ is the average fitness of the population.

$$f_i(x) = f_{S_i}(x) = \sum_{j=1}^{n+1} x_j a_{ij}$$

$$\phi(x) = \sum_{i=1}^{n+1} x_i f_i(x)$$

In the replicator equation, x_i stands for the *frequency* of species (strategy, whatsoever) i in the population. The Lotka-Volterra equation describes the *count* of species i. We can see the link between the two equation is:

$$x_i = \frac{y_i}{\sum_{j=1}^{n+1} y_j},$$

for a system with $n+1$ species.

According to [1], trajecgories under Lotka-Volterra system can be mapped to replicator dynamics by setting one of the y_i species to 1, and with the corresponding row i in the payoff matrix set to all zeros. Here, let's set $y_{n+1} = 1$, and let $a_{n+1,j} = 0, \forall j \in [1, n+1]$.

Re-writing the replicator equation under the previous setting:

$$x_i = \frac{y_i}{1 + \sum_{j=1}^{n} y_j} \iff y_i = x_i \left(1 + \sum_{j=1}^{n} y_j\right)$$

Re-writing the Lotka-Volterra equation in terms of x_i:

$$\begin{aligned}
y_i &= \frac{y_i}{1} \\
&= \frac{y_i}{y_{n+1}} \\
&= \frac{x_i \cdot \cancel{\left(1 + \sum_{j=1}^{n} y_j\right)}}{x_{n+1} \cdot \cancel{\left(1 + \sum_{j=1}^{n} y_j\right)}} \\
&= \frac{x_i}{x_{n+1}}
\end{aligned}$$

Using the quotient rule we have

$$\begin{aligned}
\dot{y_i} &= \frac{\dot{x}_i x_{n+1} - x_i \dot{x}_{n+1}}{x_{n+1}^2} \\
&= \frac{x_i [f_i(x) - \phi(x)] \cancel{x_{n+1}} - x_i \cancel{x_{n+1}} [f_{n+1}(x) - \phi(x)]}{x_{n+1}^{\cancel{2}}} \\
&= \frac{x_i}{x_{n+1}} \left(f_i(x) - f_{n+1}(x)\right) \\
&= \frac{x_i}{x_{n+1}} \left(\sum_{j=1}^{n+1} x_j a_{ij} - \sum_{j=1}^{n+1} a_{n+1,j} x_j\right) \\
&= y_i \left(x_{n+1} a_{i,n+1} + \sum_{j=1}^{n} x_j a_{ij}\right) \qquad \text{(Since } a_{n+1,j} = 0\text{)} \\
&= y_i \left(a_{i,n+1} + \sum_{j=1}^{n} a_{ij} y_j\right) x_{n+1} \\
&= y_i \left(r_i + \sum_{j=1}^{n} b_{ij} y_j\right)
\end{aligned}$$

Using the wording from [2]: "up to the factor x_{n+1} which means only a change of velocity, the Lotka-Volterra equation is just the differential equation on the simplex S_{n+1} called replicator equation.

Problem 2: Reactive strategies

Consider the Prisoner's Dilemma game. Imagine the game is played iteratively, and in each round the players choose a strategy based on the move of the opponent in the previous round. In particular, a *reactive strategy* $S(p, q)$ consists of the following moves:

- Cooperate with probability p if the opponent has cooperated in the round before; if he has defected, cooperate with probability q.

- The probabilities of defecting are then given by $1-p$, if the opponent has cooperated; $1-q$ if he has defected.

If both players have reactive strategies $S_1(p_1, q_1)$ and $S_2(p_2, q_2)$, the resulting dynamics are described by a Markov process, because in each round the new strategies are chosen in a probabilistic way based on the strategies in the previous round. The state-space of this Markov Chain is $\{CC, CD, DC, DD\}$. Here CD denotes that player one cooperates and player two defects. The transition matrix of the Markov chain is given by:

$$M = \begin{array}{c} \\ CC \\ CD \\ DC \\ DD \end{array} \begin{array}{c} \begin{array}{cccc} CC & CD & DC & DD \end{array} \\ \begin{pmatrix} p_1p_2 & p_1(1-p_2) & (1-p_1)p_2 & (1-p_1)(1-p_2) \\ q_1p_2 & q_1(1-p_2) & (1-q_1)p_2 & (1-q_1)(1-p_2) \\ p_1q_2 & p_1(1-q_2) & (1-p_1)q_2 & (1-p_1)(1-q_2) \\ q_1q_2 & q_1(1-q_2) & (1-q_1)q_2 & (1-q_1)(1-q_2) \end{pmatrix} \end{array}$$

(a) Show that M is a stochastic matrix.

A (right) stochastic matrix satisfies the following conditions:

1. It's a square matrix.
2. $0 \leq A_{ij} \leq 1, \forall i, j$
3. $\sum_j A_{ij} = 1, \forall i$

Condition 1 and 2 are trivially satisfied. Let's check condition 3 on row 1:

$$\begin{aligned} \sum_1 M_{1j} &= p_1p_2 + p_1(1-p_2) + (1-p_1)p_2 + (1-p_1)(1-p_2) \\ &= p_1p_2 + p_1 - p_1p_2 + p_2 - p_1p_2 + 1 - p_1 - p_2 + p_1p_2 \\ &= 1 \end{aligned}$$

The same calculation can be done for the other row (just substitue p_1 for q_1 and / or p_2 for q_2 accordingly on each row). Therefore, M is a stochastic matrix.

(b) See below.

Because M is regular, there exists a unique stationary distribution x. Define $r_1 = p_1 - q_1$, $r_2 = p_2 - q_2$, and set

$$s_1 = \frac{q_2r_1 + q_1}{1 - r_1r_2}, \quad \text{and} \quad s_2 = \frac{q_1r_2 + q_2}{1 - r_1r_2}.$$

and let

$$x = (s_1s_2, s_1(1-s_2), (1-s_1)s_2, (1-s_1)(1-s_2)).$$

Show that x is the stationary distribution to the Markov chain with transition matrix M.

Note: It will be sufficient to show that the first component of x solves $x_1 = \sum_j x_jM_{j1}$; the other components follow by an analogous calculation which you don't need to do.

The stationary distribution x satisfies the following equation:

$$x = xM$$

Let's show that the euqation holds by calculating $x_1 = \sum_j x_j M_{j1}$:

$$\begin{aligned}
\sum_j x_j M_{j1} &= x_1 M_{11} + x_2 M_{21} + x_3 M_{31} + x_4 M_{41} \\
&= s_1 s_2 \cdot p_1 p_2 + s_1(1-s_2) \cdot q_1 p_2 + (1-s_1)s_2 \cdot p_1 q_2 + (1-s_1)(1-s_2) \cdot q_1 q_2 \\
&= s_1 s_2 \left(p_1 p_2 - q_1 p_2 - p_1 q_2 + q_1 q_2\right) + s_1 q_1 p_2 + s_2 p_1 q_2 - s_1 q_1 q_2 - s_2 q_1 q_2 + q_1 q_2 \\
&= s_1 s_2 r_1 r_2 + s_1 q_1 r_2 + s_2 q_2 r_1 + q_1 q_2 \\
&= [((q_2 r_1 + q_1)(q_1 r_2 + q_2) r_1 r_2) + \\
&\qquad ((q_2 r_1 + q_1) \cdot q_1 r_2 \cdot (1 - r_1 r_2)) + \\
&\qquad ((q_1 r_2 + q_2) \cdot q_2 r_1 \cdot (1 - r_1 r_2)) + \\
&\qquad (q_1 q_2 \cdot (1 - r_1 r_2)^2)] \cdot \frac{1}{(1 - r_1 r_2)^2} \\
&= \frac{q_1 q_2 r_1 r_2 + q_1^2 r_2 + q_1 q_2 + q_2^2 r_1}{(1 - r_1 r_2)^2} \\
&= s_1 s_2 = x_1
\end{aligned}$$

The other components of x can be calculated in a similar way.

(c) Suppose player one plays the strategy $S_1(1,0)$, against an arbitrary reactive strategy $S_2(p2, q2)$. What is the name of strategy $S_1(1,0)$? Show that the long run expected payoff for the first player is always identical to the opponent's payoff.

The strategy $S_1(1,0)$ is called *tic-for-tac*.

In this case, we have $r_1 = 1 - 0 = 1$, and $r_2 = p_2 - q_2$ and

$$s_1 = \frac{q_2}{1 - r_2}, \quad \text{and} \quad s_2 = \frac{q_2}{1 - r_2}$$

We see that $s_1 = s_2$. The expected payoff at the stationary distribution is the same for both players.

References

[1] I. M. Bomze, "Lotka-volterra equation and replicator dynamics: New issues in classification," *Biological cybernetics*, vol. 72, no. 5, pp. 447–453, 1995.

[2] J. Hofbauer, "On the occurrence of limit cycles in the volterra-lotka equation," *Nonlinear Analysis: Theory, Methods & Applications*, vol. 5, no. 9, pp. 1003–1007, 1981.