PSET 4

Due on **Tuesday October 3, 2023 at 11:59 AM ET**

MATH 242: Mathematical Biology-Evolutionary Dynamics, Fall 2023 (Martin Nowak) Version: **1.0**

This PSET should not be turned in.

1 (100 PTS.) REPLICATOR DYNAMICS

Two species of butterflies are coevolving in a population. Species S1 has frequency x, and species S2 has frequency $1-x$. Their fitnesses are frequency-dependent with payoff matrix

$$\begin{array}{c c} & \begin{array}{cc} S1 & S2 \end{array} \\ \begin{array}{c} S1 \\ S2 \end{array} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{array} \tag{1}$$

1.A. Write down the replicator equation for $\dot{x}$. Prove that adding an arbitrary constant to either column of the payoff matrix would have no effect on the dynamics of the system.

1.B. Derive the condition under which neither pure S1 nor pure S2 is an evolutionarily stable strategy (ESS). In this scenario, what are the frequencies of S1 and S2 in the long run?

1.C. In the case of constant selection where $a = b$ and $c = d$, the two species' fitnesses are no longer frequency-dependent. Fisher's Fundamental Theorem states that, in this special case of constant selection, the time rate of change of the average fitness ϕ across species is equal to the variance in fitness across species (which implies that the average fitness ϕ will not decrease over time). Verify that this theorem holds for the case of two species.

1.D. When selection is not constant, selection can sometimes act to decrease average fitness over time. Choose a set of payoff values a, b, c, d and initial frequencies x_0 and $1-x_0$ for which the average fitness decreases. Using your favorite programming language, plot the average fitness ϕ over time to show that it indeed decreases for your chosen parameters.

1.E. When there are more than two species, the species abundances and average fitness can oscillate over time in interesting ways. Consider the three-species payoff matrix

$$\begin{array}{c c} & \begin{array}{ccc} S1 & S2 & S3 \end{array} \\ \begin{array}{c} S1 \\ S2 \\ S3 \end{array} & \begin{pmatrix} r & -1 & 1 \\ 0 & r & -1 \\ -1 & 1 & r \end{pmatrix} \end{array} \tag{2}$$

where r is the strength of cooperation within a species. For $r = 0$, use your favorite programming language to plot the species frequencies (x_1, x_2, x_3) over time, as well as the average fitness ϕ over time, from $t = 0$ to $t = 60$. Set the initial species frequencies to $(.8, .1, .1)$. Then repeat this for $r = -.5$, $r = .5$, $r = 1.5$. What differences do you see?

Solution:

1.A. Proof: The replicator equation for two strains can be written as

$$\begin{aligned} \dot{x} &= x(f_1 - \phi) && (3)\\ &= x(1-x)(f_1 - f_2) && (4)\\ &= x(1-x)[(a-c)x + (b-d)(1-x)]. && (5) \end{aligned}$$

Because the replicator dynamics depend only on $a - c$ and $b - d$, adding any constant to either column will not affect the dynamics. □

1.B. S1 is not an ESS if $f_1 \leqslant f_2$ when $x = 1 - \varepsilon$ for arbitrarily small positive ε. This means

$$\begin{aligned} f_1 - f_2 &= (a-c)(1-\varepsilon) + (b-d)\varepsilon && (6)\\ &= (a-c) - [(a-c) - (b-d)]\varepsilon && (7)\\ &\leqslant 0. && (8) \end{aligned}$$

Hence for small ε, we find that S1 is not an ESS if (1a) $a < c$, or (1b) $a = c$ and $b \leqslant d$. By symmetry, we also find that S2 is not an ESS if (2a) $d < b$, or (2b) $d = b$ and $c \leqslant a$.

If (1a) is true, then (1b) and (2b) are false, so (2a) must be true, so $a < c$ and $d < b$. These types of discoordination games are called ***chicken***, ***snowdrift***, and ***hawk-dove*** respectively. At equilibrium, we know that $0 < x < 1$ and that $\dot{x} = x(1-x)[(a-c)x + (b-d)(1-x)] = 0$, and so

$$x^* = \frac{b-d}{(b-d)+(c-a)}, \quad 1 - x^* = \frac{c-a}{(b-d)+(c-a)}. \tag{9}$$

If (1b) is true, then (1a) and (2a) are false, so (2b) must be true, so $a = c$ and $b = d$. In this scenario, both species always have equal fitness, and we call this ***neutral evolution***. Since $\dot{x} = 0$ for any frequency x, the long-run frequency x^* is the initial frequency $x(0)$.

1.C. Now f_1, f_2 are constants. In terms of the frequencies $x_1 = x$ and $x_2 = 1 - x$, we have

$$\dot{\phi} = \frac{d}{dt}[f_1 x_1 + f_2 x_2] \tag{10}$$

$$= f_1 \dot{x}_1 + f_2 \dot{x}_2 - \phi \cdot (\dot{x}_1 + \dot{x}_2) \tag{11}$$

$$= (f_1 - \phi)\dot{x}_1 + (f_2 - \phi)\dot{x}_2 \tag{12}$$

$$= (f_1 - \phi)^2 x_1 + (f_2 - \phi)^2 x_2. \tag{13}$$

This is the average squared distance of fitness from the mean, which is the variance and must be non-negative. In line 2, we used the fact that $\dot{x}_1 + \dot{x}_2 = 0$ because $x_1 + x_2 = 1$.

1.D. There are many possibilities. A simple one is a prisoner's dilemma, where $b < d < a < c$.

1.E. For $r < 0$, the species coexist at the interior equilibrium. For $r = 0$, the species cycle periodically. For $r > 0$, the time between oscillations grows increasingly large with r.

2 (100 pts.) Infection Defection

Bacteriophage $\phi 6$ is a virus that infects the *Pseudomonas phaseolicola* bacteria, using special phage enzymes to replicate intracellularly, degrade the cell membrane, and spread phage to nearby bacterial cells. Phages with the cooperator genotype C produce a full complement of enzymes which diffuse throughout the cell and can be used by other phages infecting the same cell. Phages with the defector genotype D produce much less of this resource, instead relying on the enzyme produced by nearby cooperators.

In this problem, you will use the tools of evolutionary game theory to interpret phage fitness data and to make predictions about the fate of the phage strains. You may assume that the phage population infecting each cell is very large and resembles the phage population overall. Given two phage strains, C and D, suppose we have the following linear payoff matrix:

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R & S \\ T & P \end{pmatrix} \end{array} \tag{14}$$

where $T > R > P > S$.

For example, if a single D particle infects a cell otherwise inhabited entirely by C phage, the expected number of D particles released from the cell that will later infect another cell is T.

2.A. Calculate ϕ, the average fitness of the phage population, in terms of x, the fraction of the phage population that is strain C. Then suppose we design a simple experiment to measure ϕ for various x, and a regression analysis reveals that ϕ increases linearly in x. What relationship can we deduce must exist between the entries of the payoff matrix?

2.B. If the benefit of cooperation is $b = R - S > 0$ and the cost is $c = P - S > 0$, explain why the payoff matrix above can be written equivalently with only two free parameters:

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} b-c & -c \\ b & 0 \end{pmatrix} \end{array} \tag{15}$$

where $b > c > 0$.

Then determine what proportion of cooperation x maximizes the population fitness ϕ.

2.C. Write down the replicator equation for the dynamics of x over time t, and solve for $x(t)$. What happens to $x(t)$ as $t \to \infty$? What happens to the population fitness ϕ as $t \to \infty$?

2.D. If the initial phage population is evenly split between the two strains, how long will it take the population to become 95% dominated by a single strain, in terms of b and c?

2.E. Now let there be a finite number N of phage in each cell. Given that a phage interacts with all other coinfecting phages, including itself, calculate the new difference in strain fitnesses, $f_C - f_D$. Argue that the cooperating strain C will survive if and only if $b/c > N$. Is cooperation more likely in host cells with few phage or in host cells with many phage?

Solution:

2.A.

$$\begin{aligned} \phi &= Rx^2 + (S+T)x(1-x) + P(1-x)^2 \qquad (16)\\ &= (R-S-T-P)x^2 + (S+T-2P)x + P. \qquad (17) \end{aligned}$$

If ϕ is a linear function of x, then the quadratic term must vanish, so $R + P = S + T$. This is sufficient to ensure that $S + T - 2P = R - P > 0$, so that ϕ increases in x.

2.B. We can subtract P from all entries of the payoff matrix without changing the dynamics, as shown in **1.A.**. Then the entries of $R - P = (R - S) - (P - S) = b - c$, and $S - P = -c$, and $T - P = R - S = b$ because of the condition from **2.A.**, and $P - P = 0$.

The average fitness is $\phi = (b - c)x$. Given that $b > c$, this achieves the global maximum of $\phi = (b - c)$ at $x = 1$, which is full cooperation.

2.C. Because $f_1 - f_2 = -c$, the replicator equation is a logistic equation, $\dot{x} = -cx(1-x)$. This differential equation can be solved via separation of variables to give

$$x(t) = \left(1 + e^{ct}\left(\frac{1}{x(0)} - 1\right)\right)^{-1}. \tag{18}$$

Since $c > 0$, as $t \to \infty$ we know $e^{ct} \to \infty$ so that $x(t) \to 0$. In other words, cooperation goes extinct. Then $\phi = (b-c)x \to 0$, so the mean population fitness also goes to zero.

2.D. If $x(0) = 1/2$, then we want to find the time t at which $x(t) = 1/20$. To do this, we solve

$$x(t) = \left(1 + e^{ct}(\frac{1}{1/2} - 1)\right)^{-1} = 1/20. \tag{19}$$

Simplifying this gives $1 + e^{ct} = 20$, which has the solution $t = \frac{1}{c}\ln 19$.

2.E. A cooperating phage in a host cell with $N-1$ other phages on average shares the cell with $1+x(N-1)$ cooperating phages, including itself, so its expected fitness is

$$f_C = b\frac{1 + x(N-1)}{N} - c. \tag{20}$$

A defecting phage in a host cell with $N-1$ other phages on average shares the cell with just $x(N-1)$ cooperating phages, and so its expected fitness is

$$f_D = b\frac{x(N-1)}{N}. \tag{21}$$

The cooperating strain survives if and only if $f_C > f_D$, which is true when

$$f_C - f_D = b/N - c > 0 \tag{22}$$

which is equivalent to $b/c > N$ as desired. This implies that cooperation is more likely in a host cell with few phage, such that the minimum benefit-to-cost threshold is lowered relative to a host cell with many phage. Note that in the limit of many phage $N \to \infty$, cooperation cannot survive, as we saw in the previous part of this problem.

3 (100 PTS.) SUBOPTIMAL COEXISTENCE

Two species are evolving over time with frequencies x and $1-x$, and with fitnesses $f_1(x)$ and $f_2(x)$ respectively, according to the standard replicator dynamic

$$\dot{x} = x(1-x)(f_1(x) - f_2(x)). \tag{23}$$

You discover that both species stably coexist at frequencies x^* and $1-x^*$ where $0 < x^* < 1$, yet the average fitness $\phi(x)$ is minimized at this ESS, such that $\phi'(x^*) = 0$ and $\phi''(x^*) \geqslant 0$. Show that

$$\frac{d}{dx}\ln\left|\frac{df_2}{df_1}\right| \geqslant 8 \tag{24}$$

at $x = x^*$. It may help to compute $\frac{f_2(x^*)}{f_1(x^*)}$ and $\frac{f_2'(x^*)}{f_1'(x^*)}$ in terms of x^*, and to verify that $f_1'(x^*) < 0 < f_2'(x^*)$.

Solution:

First, note that the desired expression can be expanded to give

$$\frac{d}{dx}\ln\left|\frac{df_2}{df_1}\right| = \frac{d}{dx}\ln\left|\frac{f_2'(x)}{f_1'(x)}\right| \tag{25}$$

$$= -\frac{f_1''(x)}{f_1'(x)} + \frac{f_2''(x)}{f_2'(x)}. \tag{26}$$

This fitnesses of both species must be equal at the coexistence frequency, so $f_2(x^*)/f_1(x^*) = 1$. Since the coexistence equilibrium is stable, we must also have the inequality $f_1'(x^*) < f_2'(x^*)$. Differentiating the average fitness $\phi(x) = f_1(x)x + f_2(x)(1-x)$ with respect to x gives that

$$\phi'(x^*) = f_1'(x^*)x^* + f_2'(x^*)(1-x^*) + [f_1(x^*) - f_2(x^*)] = 0. \tag{27}$$

Since $f_1(x^*) - f_2(x^*) = 0$, we can rearrange this equation to find the ratio of first derivatives,

$$\frac{f_2'(x^*)}{f_1'(x^*)} = -\frac{x^*}{1-x^*} < 0. \tag{28}$$

Hence $f_1'(x^*)$ and $f_2'(x^*)$ have opposite sign, from which we have $f_1'(x^*) < 0 < f_2'(x^*)$. Finally,

$$\phi''(x^*) = f_1''(x^*)x^* + f_2''(x^*)(1-x^*) + 2[f_1'(x^*) - f_2'(x^*)] \geqslant 0. \tag{29}$$

Dividing this equation by the positive quantity $(1-x^*)f_2'(x^*)$, we now know that

$$\frac{f_1''(x^*)}{f_2'(x^*)}\frac{x^*}{1-x^*} + \frac{f_2''(x^*)}{f_2'(x^*)} + \left[\frac{f_1'(x^*)}{f_2'(x^*)} - 1\right]\frac{2}{1-x^*} \geqslant 0. \tag{30}$$

Substituting in our expression for $f_2'(x^*)/f_1'(x^*) = -x^*/(1-x^*)$, we obtain the inequality

$$-\frac{f_1''(x^*)}{f_1'(x^*)} + \frac{f_2''(x^*)}{f_2'(x^*)} \geqslant \frac{2}{x^*(1-x^*)}. \tag{31}$$

At $x^* = 1/2$, the function $\frac{2}{x^*(1-x^*)}$ achieves its minimum value, $\frac{2}{(1/2)\cdot(1-1/2)} = 8$. This gives the desired result.