

Biomath 202 2013 Exam

SIMON LEE

July 2024

1 Answer

1.1 Question 1

1) First, let's express the replicator equation for p_A in terms of just p_A and $\Delta\pi = \pi_A - \pi_B$:

$$\begin{aligned}\frac{dp_A}{dt} &= p_A(\pi_A - \bar{\pi}) \\ &= p_A(\pi_A - (p_A\pi_A + p_B\pi_B)) \\ &= p_A(\pi_A - (p_A\pi_A + (1 - p_A)\pi_B)) \quad (\text{since } p_A + p_B = 1) \\ &= p_A(\pi_A - p_A\pi_A - \pi_B + p_A\pi_B) \\ &= p_A((1 - p_A)\pi_A - (1 - p_A)\pi_B) \\ &= p_A(1 - p_A)(\pi_A - \pi_B) \\ &= p_A(1 - p_A)\Delta\pi\end{aligned}$$

2) The analogous equation for p_B can be derived similarly:

$$\begin{aligned}\frac{dp_B}{dt} &= p_B(\pi_B - \bar{\pi}) \\ &= p_B(\pi_B - (p_A\pi_A + p_B\pi_B)) \\ &= p_B(\pi_B - ((1 - p_B)\pi_A + p_B\pi_B)) \\ &= p_B(\pi_B - \pi_A + p_B\pi_A - p_B\pi_B) \\ &= p_B((1 - p_B)\pi_B - (1 - p_B)\pi_A) \\ &= p_B(1 - p_B)(\pi_B - \pi_A) \\ &= -p_B(1 - p_B)\Delta\pi\end{aligned}$$

3) For the case of k different types (A, B, C, ..., k) of individuals, the replicator equation for type i would be:

$$\frac{dp_i}{dt} = p_i(\pi_i - \bar{\pi})$$

where $\bar{\pi} = \sum_{j=1}^k p_j\pi_j$ is the mean payoff for the whole population.

4) When $k > 2$, the replicator equation for p_A cannot be simplified to involve only p_A and $\Delta\pi = \pi_A - \pi_B$. This is because:

$$\begin{aligned}\frac{dp_A}{dt} &= p_A(\pi_A - \bar{\pi}) \\ &= p_A(\pi_A - (p_A\pi_A + p_B\pi_B + \sum_{i \neq A, B} p_i\pi_i))\end{aligned}$$

The term $\sum_{i \neq A, B} p_i\pi_i$ cannot be expressed in terms of just p_A and $\Delta\pi$ when there are more than two types of individuals. Therefore, the simplification is not possible for $k > 2$.

1.2 Question 2:

Let's derive Wright's equation for a two-state system ($k=2$) and discuss its similarities and differences with the population genetics derivation. I'll use LaTeX to show all mathematical steps.

2. Deriving Wright's equation:

Starting from the replicator equation we derived earlier:

$$\frac{dp_A}{dt} = p_A(1 - p_A)\Delta\pi$$

Where $\Delta\pi = \pi_A - \pi_B$.

To derive Wright's equation, we need to express this in terms of mean fitness \bar{w} . In evolutionary game theory, fitness is often equated with payoff, so we can consider $\bar{w} = \bar{\pi}$.

$$\begin{aligned}\bar{w} &= p_A\pi_A + (1 - p_A)\pi_B \\ \frac{\partial \bar{w}}{\partial p_A} &= \pi_A - \pi_B = \Delta\pi\end{aligned}$$

Now, let's consider the change in p_A over one generation:

$$\begin{aligned}\Delta p_A &= p_{A,t+1} - p_{A,t} \\ &\approx \frac{dp_A}{dt} \quad (\text{for small time steps}) \\ &= p_A(1 - p_A)\Delta\pi \\ &= p_A(1 - p_A)\frac{\partial \bar{w}}{\partial p_A}\end{aligned}$$

This is Wright's equation for a two-state system:

$$\Delta p_A = p_A(1 - p_A)\frac{\partial \ln \bar{w}}{\partial p_A}$$

Note that we've used $\frac{\partial \ln \bar{w}}{\partial p_A}$ instead of $\frac{\partial \bar{w}}{\partial p_A}$ because:

$$\frac{\partial \ln \bar{w}}{\partial p_A} = \frac{1}{\bar{w}} \frac{\partial \bar{w}}{\partial p_A}$$

And in the context of relative fitness, we can consider $\bar{w} = 1$, making these expressions equivalent. Similarities with population genetics derivation:

1. Both involve changes in allele/type frequencies over time.
2. Both consider fitness differences as driving forces of evolution.
3. The basic structure of $p(1 - p)$ multiplied by a fitness term is present in both.

Differences from population genetics derivation:

1. Population genetics typically involves discrete generations, while this model uses continuous time.
2. The population genetics model often includes separate terms for homozygotes and heterozygotes, which are not present here.
3. In population genetics, we often deal with specific fitness values for genotypes, while here we use a more general payoff function.
4. The population genetics version might include terms for mutation or migration, which are not present in this simpler model.

5. This model is more focused on game-theoretic interactions and payoffs, while population genetics often deals with fixed fitness values.

The derivation here is more general and applicable to various types of interactions beyond genetic inheritance, making it useful for studying evolutionary game theory and other complex population dynamics.

1.3 Question 3

For the special case where $\pi_{A \rightarrow B} = \pi_{B \rightarrow A}$, let's express the replicator equation in terms of $\frac{\partial \bar{\pi}}{\partial p_A}$: From part 1, we have:

$$\frac{dp_A}{dt} = p_A(1 - p_A)\Delta\pi$$

Now, let's calculate $\frac{\partial \bar{\pi}}{\partial p_A}$:

$$\begin{aligned}\bar{\pi} &= p_A\pi_A + (1 - p_A)\pi_B \\ &= p_A(p_A\pi_{A \rightarrow A} + (1 - p_A)\pi_{A \rightarrow B}) + (1 - p_A)(p_A\pi_{B \rightarrow A} + (1 - p_A)\pi_{B \rightarrow B}) \\ \frac{\partial \bar{\pi}}{\partial p_A} &= (2p_A\pi_{A \rightarrow A} + (1 - 2p_A)\pi_{A \rightarrow B}) - (p_A\pi_{B \rightarrow A} + (1 - 2p_A)\pi_{B \rightarrow B}) \\ &= p_A(\pi_{A \rightarrow A} - \pi_{B \rightarrow A}) + (1 - p_A)(\pi_{A \rightarrow B} - \pi_{B \rightarrow B}) \\ &= \Delta\pi \quad (\text{given that } \pi_{A \rightarrow B} = \pi_{B \rightarrow A})\end{aligned}$$

Therefore, the replicator equation can be expressed as:

$$\frac{dp_A}{dt} = p_A(1 - p_A)\frac{\partial \bar{\pi}}{\partial p_A}$$

Comparison to Wright's equation: This form is identical to Wright's equation derived in part 2:

$$\Delta p_A = p_A(1 - p_A)\frac{\partial \ln \bar{w}}{\partial p_A}$$

This implies that $\bar{\pi}$ and $\ln \bar{w}$ are equivalent in this context. It suggests that the average payoff $\bar{\pi}$ is directly related to the logarithm of average fitness $\ln \bar{w}$. This aligns with the exponential fitness definition from class, where fitness is often defined as $w = e^\pi$, making $\ln w = \pi$.

1.4 Question 4

a) Expression for $\Delta\pi$: From the interaction matrix:

$$I = \begin{bmatrix} b - c & -c \\ b & 0 \end{bmatrix}$$

We can calculate $\Delta\pi$:

$$\begin{aligned}\pi_A &= p_A(b - c) + (1 - p_A)(-c) = p_A b - c \\ \pi_B &= p_A b + (1 - p_A)(0) = p_A b \\ \Delta\pi &= \pi_A - \pi_B = (p_A b - c) - p_A b = -c\end{aligned}$$

$\Delta\pi = -c$, which only depends on the cost c and is independent of p_A and p_B . b) Solving the replicator equations:

$$\begin{aligned}\frac{dp_A}{dt} &= -cp_A(1 - p_A) \\ \frac{dp_A}{p_A(1 - p_A)} &= -cdt \\ \int \frac{dp_A}{p_A(1 - p_A)} &= -c \int dt \\ \ln\left(\frac{p_A}{1 - p_A}\right) &= -ct + K \\ \frac{p_A}{1 - p_A} &= Ae^{-ct} \quad \text{where } A = e^K \\ p_A &= \frac{Ae^{-ct}}{1 + Ae^{-ct}}\end{aligned}$$

And since $p_B = 1 - p_A$:

$$p_B = \frac{1}{1 + Ae^{-ct}}$$

c) Behavior of the solution: Early times ($t \rightarrow 0$): $p_A \approx \frac{A}{1+A}$, a constant determined by initial conditions. Late times ($t \rightarrow \infty$): $p_A \rightarrow 0$ and $p_B \rightarrow 1$ Population B (selfish individuals) will go to fixation, regardless of parameter values (as long as $c > 0$). This is because altruistic behavior (type A) always incurs a cost without direct benefit to itself in this model.

1.5 Question 5

a) Modified interaction matrix:

$$I = \begin{bmatrix} b - c & -c + rb_k \\ b & 0 \end{bmatrix}$$

b) $\Delta\pi$ for this case:

$$\begin{aligned} \pi_A &= p_A(b - c) + (1 - p_A)(-c + rb_k) = p_A b - c + (1 - p_A)rb_k \\ \pi_B &= p_A b + (1 - p_A)(0) = p_A b \\ \Delta\pi &= \pi_A - \pi_B = -c + (1 - p_A)rb_k \end{aligned}$$

c) Inequality for $\Delta\pi$ to be positive or negative: $\Delta\pi > 0$ when:

$$-c + (1 - p_A)rb_k > 0$$

$$rb_k > \frac{c}{1 - p_A}$$

This is a version of Hamilton's inequality. For $\Delta\pi$ to be positive (favoring altruism), the product of relatedness (r) and indirect benefit (b_k) must exceed the cost (c) divided by the proportion of non-A individuals. d) Effect on trajectories: If $\Delta\pi > 0$, $dp_A/dt > 0$, and the proportion of altruists (type A) will increase over time. If $\Delta\pi < 0$, $dp_A/dt < 0$, and the proportion of altruists will decrease. If $\Delta\pi = 0$, there will be a stable equilibrium where both types coexist. The trajectories will now depend on the values of r , b_k , and c , potentially allowing for the evolution and maintenance of altruism under certain conditions, unlike in the previous model where selfish behavior always won out.

1.6 Question 6

Adding white noise $\eta(t)$ to the replicator equations from part 1:

$$\frac{dp_A}{dt} = p_A(1 - p_A)\Delta\pi + \eta(t)$$

This can be considered a Langevin equation. Here's why:

1. It contains a deterministic part: $p_A(1 - p_A)\Delta\pi$
2. It includes a stochastic term: $\eta(t)$, which represents random fluctuations

The general form of the corresponding Fokker-Planck equation for the probability distribution $P(p_A, t)$ is:

$$\frac{\partial P}{\partial t} = -\frac{\partial}{\partial p_A}[A(p_A)P] + \frac{1}{2}\frac{\partial^2}{\partial p_A^2}[B(p_A)P]$$

Where:

- $A(p_A)$ is the drift term: $A(p_A) = p_A(1 - p_A)\Delta\pi$
- $B(p_A)$ is the diffusion term, related to the intensity of the noise

For the example in part 4, where $\Delta\pi = -c$, the Fokker-Planck equation becomes:

$$\frac{\partial P}{\partial t} = \frac{\partial}{\partial p_A}[cp_A(1 - p_A)P] + \frac{1}{2}\frac{\partial^2}{\partial p_A^2}[B(p_A)P]$$

The equilibrium solution for this probability distribution, assuming $B(p_A)$ is constant (say, B), is:

$$P_{eq}(p_A) \propto \exp\left(-\frac{2c}{B}[p_A \ln p_A + (1 - p_A) \ln(1 - p_A)]\right)$$

This is a beta distribution, which peaks at $p_A = 0$, consistent with the deterministic solution where selfish individuals (type B) go to fixation.

1.7 Question 7

Based on the Itzkovic-Alon paper, the expected number of triangle motifs in a network with N nodes and L links maintained over time t can be expressed as:

$$\text{Expected triangles} = \binom{N}{3} \int_0^t \int_0^t F(x, y) F(x, z) F(y, z) dx dy dz$$

Where $F(x, y)$ is the connectivity function representing the probability that a link formed at time x is still present at time y .

To modify the interaction matrix I to include this information:

1. Introduce a time-dependent term: $I(t)$ instead of a static I .
2. For each entry $I_{ij}(t)$, multiply by a factor representing the probability of a three-way interaction:

$$I_{ij}(t) = I_{ij} \cdot P_{triangle}(t)$$

Where $P_{triangle}(t)$ is derived from the integral above, normalized by the total number of possible triangles:

$$P_{triangle}(t) = \frac{\text{Expected triangles}}{\binom{N}{3}}$$

3. This modification allows the payoffs to vary over time based on the likelihood of three-way interactions occurring.
4. The entries of $I(t)$ would now represent expected payoffs considering both direct interactions and the influence of potential mediators or "policing" effects.
5. The time dependence in $I(t)$ would make the replicator equations non-autonomous, potentially leading to more complex dynamics in the system.

This approach incorporates the network structure and temporal aspects of interactions into the game-theoretic framework, allowing for a more nuanced analysis of complex social systems with higher-order interactions.