

Comprehensive Exam 2013
Biomath 202: The Structure, Function, and Evolution of Biological Systems

A population with two types of individuals, A and B, can have interactions between members of group A and B as well as within groups A and B. The outcomes of these interactions can be represented by an interaction matrix

$$I = \begin{bmatrix} \pi_{A \rightarrow A} & \pi_{B \rightarrow A} \\ \pi_{A \rightarrow B} & \pi_{B \rightarrow B} \end{bmatrix}$$

where $\pi_{A \rightarrow A}$ is the payoff to an A individual from an interaction between two A's, $\pi_{B \rightarrow A}$ is the payoff to an A individual from an interaction between an A and a B, $\pi_{A \rightarrow B}$ is the payoff to a B individual from an interaction between an A and a B, and $\pi_{B \rightarrow B}$ is the payoff to a B individual from an interaction between two B's. These types of matrices are common in game theory and models of kin selection, sex ratios, competition over resources, and many others. Let p_A be the proportion of A individuals and p_B be the proportion of B individuals in the population. The payout that is on average expected for an A individual is defined to be π_A , and the payout expected for a B individual is defined to be π_B . Note that for random interactions, we can find these expected values as

$$I \cdot p = \begin{bmatrix} \pi_{A \rightarrow A} & \pi_{B \rightarrow A} \\ \pi_{A \rightarrow B} & \pi_{B \rightarrow B} \end{bmatrix} \begin{bmatrix} p_A \\ p_B \end{bmatrix} = \begin{bmatrix} \pi_{A \rightarrow A} p_A + \pi_{B \rightarrow A} p_B \\ \pi_{A \rightarrow B} p_A + \pi_{B \rightarrow B} p_B \end{bmatrix} \equiv \begin{bmatrix} \pi_A \\ \pi_B \end{bmatrix}$$

The dynamics of the frequencies for A and B individuals are typically given by the replicator equations

$$\frac{dp_A}{dt} = p_A(\pi_A - \bar{\pi}) \quad \text{and} \quad \frac{dp_B}{dt} = p_B(\pi_B - \bar{\pi})$$

where $\bar{\pi}$ is the mean payoff for the whole population of A and B individuals taken together, and it is assumed that all else is equal for the populations of A and B individuals, including equivalent fitness for A and B individuals when no interactions are allowed.

- Express the replicator equation for p_A in terms of just p_A and $\Delta\pi = \pi_A - \pi_B$. Derive the analogous equation for p_B . What is the replicator equation for the case that there are k different types (A, B, C, ..., k) of individuals? Can the replicator equation for p_A be simplified to involve only p_A and $\Delta\pi = \pi_A - \pi_B$ when $k > 2$?
- For a two-state ($k=2$) system, derive Wright's equation

$$\Delta p_A = p_{A,t+1} - p_{A,t} = p_A (1 - p_A) \frac{\partial \ln \bar{w}}{\partial p_A} \leftarrow \bar{\pi}$$

This derivation should be analogous to (but not the same as) our derivation in class for population genetics. Discuss similarities and differences between that derivation, which involved two alleles and both homozygotes and heterozygotes, and the one here.

- Express your answer to part 1 for the replicator equation in terms of $\partial \bar{\pi} / \partial p_A$ for the special case that $\pi_{A \rightarrow B} = \pi_{B \rightarrow A}$. How does this equation compare to Wright's equation in part 2? What does this imply about the relationship between the average payoff $\bar{\pi}$ and the average fitness \bar{w} ? This relates to different definitions of fitness from class.
- One of the simplest models of altruism/cooperation is that individuals of type A give away a resource or benefit, b , in an interaction at a cost, c , to themselves, while type B individuals are selfish/defectors who never give away anything but will accept benefits/resources from type A individuals. In this case, the interaction matrix becomes

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

Find an expression for $\Delta \pi$ that only depends on the cost, c , and is independent of p_A and p_B . For this case, solve the replicator equations from part 1 exactly and plot by hand the trajectories of p_A and p_B as a function of time, $t: 0 \rightarrow \infty$. How does the solution behave in the limit of early times and the limit of late times? Will either population (A or B) go to fixation? Which one, and does it depend on the parameter values?

- Now consider a variation on the above system in which r is the chance that any given interaction involves related individuals, irrespective of whether the individuals are type A or type B. When an individual of type A interacts with an individual of type B and these two individuals are related, there is a direct benefit, b , that is received by the B individual, as before, and there is also an indirect benefit, b_k , for some genes in the A individual because the interaction helps to reproduce those genes it shares with the B individual and thus for those genes to have a higher fitness. The magnitude of b_k can be related to the degree of relatedness and thus the expected number of genes in common. How could you modify the interaction matrix, I , from part 4 to account for this? What is $\Delta \pi$ for this case? Derive an inequality for the parameters to determine whether $\Delta \pi$ is positive or negative. This is a version of what is known as Hamilton's inequality. How does this determine the trajectories from the replicator equation?
- Add white noise $\eta(t)$ to the replicator equations in part 1. Can this newly

formed equation be considered a Langevin equation? Explain. If so, what is the general form of the corresponding Fokker-Planck equation for the probability distribution, and what is the equilibrium solution for this probability distribution for the example in part 4?

7. For more complex social systems, three-way (and higher-order) interactions often occur, such that mediators or "policing" is involved. In this case, all three individuals need to be spatially close enough to one another to interact. Consider each individual to be a node, an interaction to be a link, and a three-way interaction to be a triangle motif in which three individuals (nodes) are all interacting (links) with one another connected. Based on the Itzkoviz-Alon paper, write down how many triangle motifs are expected to occur if there are N total individuals (nodes), and L interactions (links) that have happened within some time t when all interactions are maintained over that time. You can leave your answer in integral form with the connectivity functions $F(x,y)$ being unspecified. Discuss how the interaction matrix, I , might be modified to include this information. You do not need to actually write down a new interaction matrix.