1 REPLICA\nTOR EQUATION

The replicator equation for $N$ strategic types with frequencies $x_i$ for $i = 1, \ldots, N$ is given by:

$$\dot{x}_i = x_i (\pi_i - \bar{\pi}),$$

where $\pi_i$ is the payoff of type $i$ and $\bar{\pi} = \sum_i x_i \pi_i$ denotes the average population payoff. If interactions occur among pairs of individuals (and not in larger groups), the payoffs are given by a matrix $A = [a_{ij}]$, where the element $a_{ij}$ specifies the payoff of an individual of type $i$ interacting with an individual of type $j$. In that case the replicator equation can be written as

$$\dot{x}_i = x_i ((Ax)_i - x^T A x),$$

using $\pi_i = (Ax)_i$, $\bar{\pi} = x^T A x$ and $x = (x_1, \ldots, x_d)^T$ denotes the current state of the population.

1. Proof the 'quotient rule':

$$\frac{\dot{x}_i}{\dot{x}_j} = \frac{x_i (\pi_i - \bar{\pi})}{x_j (\pi_j - \bar{\pi})}.$$  

2. Prove that adding an arbitrary constant to column $j$ of the payoff matrix $A$ does not change the replicator dynamics.

3. Multiply all elements of the payoff matrix by a constant $\lambda > 0$. What are the effects on the replicator dynamics (time scale, equilibria, stability)? What about $\lambda < 0$?

4. Consider the quantity $L = \frac{x_m x_n}{x_k x_l}$ with distinct $m, n, k, l$. Under what conditions, in terms of the payoffs $a_{ij}$, is $L$ a constant of motion, i.e. conserved over time?

2 FIXATION PROBABILITIES

Consider the frequency dependent Moran process in an unstructured (well-mixed) population of fixed size $N$ consisting of two types $A, B$ and with payoff matrix

$$\begin{pmatrix} a & b \\ c & d \end{pmatrix}.$$ 

If there are $i$ individuals of type $A$ (and $(N - i)$ of type $B$), the transition probabilities are given by

$$T_i^+ = \frac{if_A}{if_A + (N - i)f_B} \frac{N - i}{N},$$

$$T_i^- = \frac{(N - i)f_B}{if_A + (N - i)f_B} \frac{i}{N}.$$
where \( f_j = 1 - w + w \pi_j \) indicates the fitness of a type \( j \) individual. \( w \) is the selection strength and 
\[
\pi_A = [(i - 1)a + (N - i)b]/(N - 1), \quad \pi_B = [i c + (N - 1 - i)d]/(N - 1)
\]
denote the average payoffs of \( A \)'s and \( B \)'s in a population with \( i \) \( A \)'s. Using the recursion

\[
\rho_i = T_i^+ \rho_{i+1} + T_i^- \rho_{i-1} + (1 - T_i^+ - T_i^-)\rho_i,
\]
together with the boundary conditions \( \rho_0 = 0 \) (\( A \)'s will never fixate as there are none to begin with) and \( \rho_N = 1 \) (\( A \)'s have already fixated), the fixation probability of a single \( A \) mutant (all other \( N - 1 \) individuals are of type \( B \)) is

\[
\rho_1 = \frac{1}{N - 1} \prod_{k=1}^{N-1} \gamma_i,
\]
with \( \gamma_i = T_i^- / T_i^+ \).

1. Determine the fixation probability of \( A \)'s in a population with \( i \) individuals of type \( A \), \( \rho_i \).

2. Determine the fixation probability of a single \( B \), \( \hat{\rho}_{N-1} = 1 - \rho_{N-1} \).

Note: the index still denotes the number of type \( A \) individuals in the population.

3 \textbf{Fixation times}

In order to characterize evolutionary dynamics in finite populations a complementary measure to fixation probabilities are fixation times, i.e. the average time until one type has taken over the entire population. In case of two types \( A, B \), there are three distinct fixation times that are relevant:

a. The average time \( t_i \) until \textit{either one} of the two absorbing states (all \( A \) or all \( B \)), is reached when starting with \( i \) individuals of type \( A \). This is the unconditional fixation time or absorption time.

b. The conditional fixation time \( t_i^A \) specifies the average time it takes to reach the absorbing state with all \( A \)'s when starting with \( i \) \( A \)'s. The time \( t_i^A \) increases for smaller \( i \) (i.e. increasing initial distance from all \( A \)). If fixation of \( A \) is almost certain, \( t_i^A \) approaches the unconditional fixation time \( t_i \). Of particular interest is \( t_1^A \), which denotes the average time it takes a single \( A \) to take over a \( B \) population.

c. In analogy to \( t_i^A \), the conditional fixation time \( t_i^B \) represents the average time to reach the absorbing state with all \( B \)'s when starting with \( i \) \( A \)'s (and \( N - i \) \( B \)'s). \( t_i^B \) decreases with increasing \( i \), i.e. with increasing initial distance from all \( A \).

A remarkable and rather surprising symmetry of the Moran process (in fact, of any process where \( i \) changes at most by 1) is the equality \( t_i^A = t_{N-1}^B \), i.e. the conditional fixation time of a single \( A \) is the same as that of a single \( B \) – independent of the actual game! However, this symmetry only holds when starting with a single \( A \) or \( B \), respectively. In general \( t_i^A \neq t_{N-1}^B \) for \( i > 1 \).

1. Unconditional fixation times: the recursion is given by

\[
\begin{align*}
t_i &= T_i^+ t_{i+1} + T_i^- t_{i-1} + (1 - T_i^+ - T_i^-)t_i + 1 \\
&= T_i^+ (t_{i+1} + 1) + T_i^- (t_{i-1} + 1) + (1 - T_i^+ - T_i^-)(t_i + 1)
\end{align*}
\]

(4)

i. Calculate \( t_1 \) given the boundary conditions \( t_0 = t_N = 0 \), which state that fixation has already occurred.

ii. \textit{optional} Calculate \( t_i \).
2. Conditional fixation times

i. Derive a recursive relation for the conditional fixation time, $t_A^1$.

*Note:* To account for the fact that the $A$ type reaches fixation, the recursion for $t_i$, Eq. (4), must be modified to include the fixation probabilities $\rho_i$, $\rho_{i-1}$ and $\rho_{i+1}$. Special care is required when dealing with the fact that for each iteration one time step has elapsed, c.f. the second form of Eq. (4).

ii. Calculate $t_A^1$ using the boundary conditions $\rho_0 t_A^0 = \rho_N t_A^N = 0$ because $\rho_0 = 0$ ($A$’s cannot fixate) and $t_A^N = 0$ ($A$’s have already fixated).

iii. *optional* Calculate $t_i^A$.

3. *Bonus:* Symmetry

Show that $t_A^1 = t_B^{N-1}$ is true. There are at least two approaches to this problem:

i. based on analogous calculations (or symmetry arguments) determine the conditional fixation time of a single $B$ type, $t_B^{N-1}$, and show their equality.

ii. consider the discrete time Markov chain on the state space $i = 0, 1, \ldots, N$ and proof the symmetry based on the expected time spent in each state on the way to fixation.