

### Problem 1: Weak selection

Consider the general two-strategy game

$$\begin{array}{cc} A & B \\ A & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \\ B & \end{array}$$

in a finite population of size  $N$ . Assume the population evolves according to an unstructured Moran process.

- (a) Show that for weak selection,  $w \ll 1$ , the fixation probability of strategy  $A$  is given by

$$\rho_A \approx \frac{1}{N} \frac{1}{1 - (\alpha N - \beta)w/6}$$

with  $\alpha = a + 2b - c - 2d$  and  $\beta = 2a + b + c - 4d$ .

You can use the following formulae:

- (i) For small  $w$ , one can approximate  $\prod_{i=1}^k (1 - wx_i) \approx 1 - w \sum_{i=1}^k x_i$ .
- (ii) For small  $w$ , it holds  $\frac{1-wy}{1-wz} \approx 1 - w(y - z)$ .
- (iii)  $\sum_{k=1}^N \sum_{i=1}^k i = N(N+1)(N+2)/3!$ .

(3 Points)

Now consider the specific game

$$\begin{array}{cc} A & B \\ A & \begin{pmatrix} 20 & 2 \\ 17 & 1 \end{pmatrix} \\ B & \end{array} := \begin{pmatrix} a & b \\ c & d \end{pmatrix}$$

- (b) Decide for which  $N$  strategies  $A$  and  $B$  are evolutionarily stable in the limit of weak selection.  
(1 Point)

- (c) Compute for which  $N$  strategy  $A$  is risk dominant in the limit of weak selection.  
(1 Point)

1a)  $i :=$  no. of type  $A$  individuals.

$$\frac{g_i}{f_i} = \frac{1-w + wG_i}{1-w + wF_i} = \frac{1-w(1-G_i)}{1-w(1-F_i)} \approx 1 - w(F_i - G_i) \text{ for } w \ll 1.$$

$$\rho_A = \frac{1}{1 + \sum_{k=1}^{N-1} \prod_{i=1}^k \left( \frac{g_i}{f_i} \right)} \approx \frac{1}{1 + \sum_{k=1}^{N-1} \prod_{i=1}^k [1 - w(F_i - G_i)]} \approx \frac{1}{1 + \sum_{k=1}^{N-1} \left[ 1 - w \sum_{i=1}^k (F_i - G_i) \right]} \text{ for } w \ll 1.$$

$$F_i - G_i = \frac{(i-1)a + (N-i)b}{N-1} - \frac{ic + (N-i-1)d}{N-1} = \frac{ia - a + Nb - ib - ic - Nd + id + d}{N-1}$$

$$= \frac{i(a-b-c+d) + N(b-d) - a+d}{N-1}$$

$$= \underbrace{i \frac{(a-b-c+d)}{N-1}}_x + \underbrace{\frac{N(b-d) - a+d}{N-1}}_y$$

$$\begin{aligned}
1 + \sum_{k=1}^{N-1} \left[ 1 - w \sum_{i=1}^k (F_i - G_i) \right] &= 1 + \sum_{k=1}^{N-1} 1 - w \sum_{k=1}^{N-1} \sum_{i=1}^k (F_i - G_i) \\
&= N - w \sum_{k=1}^{N-1} \sum_{i=1}^k (F_i - G_i) \\
&= N - w \sum_{k=1}^{N-1} \sum_{i=1}^k (ix + y) \\
&= N - w \left[ x \sum_{k=1}^{N-1} \sum_{i=1}^k i + y \sum_{k=1}^{N-1} \sum_{i=1}^k 1 \right] \\
&= N - w \left[ x \frac{(N-1)N(N+1)}{3!} + y \frac{N(N-1)}{2} \right] \\
&= N - w \left[ \frac{(a-b-c+d)}{N-1}, \frac{(N-1)N(N+1)}{6} + \frac{N(b-d)-ad}{N-1}, \frac{N(N-1)}{2} \right] \\
&= N - w \left[ \frac{(a-b-c+d)N(N+1)}{6} + \frac{N(bN-dN)-N(-ad)}{2} \right] \\
&= N - \frac{wN}{6} [(a-b-c+d)(N+1) + 3bN - 3dN - 3a + 3d] \\
&= N - \frac{wN}{6} (aN - bN - cN + dN + a - b - c + d + 3bN - 3dN - 3a + 3d) \\
&= N - \frac{wN}{6} [N(a+2b-c-2d) - (2a+b+c-4d)] = N - \frac{wN}{6} (aN - \beta) \\
\therefore P_A = \frac{1}{1 + \sum_{k=1}^{N-1} T_i = \left( \frac{g_i}{f_i} \right)} &= \frac{1}{N - \frac{wN}{6} (aN - \beta)} = \frac{1}{N} \frac{1}{1 - \frac{w}{6} (aN - \beta)}
\end{aligned}$$

1b) A is ESS<sub>N</sub> if

$$\begin{aligned}
i. \quad c(N-1) &< b + a(N-2) \\
ii. \quad d(N-2) + c(2N-1) &< b(N+1) + a(2N-4)
\end{aligned}$$

$$i. 17(N-1) < 2 + 20(N-2)$$

$$\begin{aligned}
3N &> 40 - 2 - 17 \\
N &> 7
\end{aligned}$$

$$\begin{aligned}
ii. \quad N-2 + 34N - 17 &< 2N+2 + 40N - 80 \\
7N &> 59 \\
N &> 8.4
\end{aligned}$$

Made with Geogebra.  $\therefore A$  is ESS<sub>N</sub> for  $N \geq 9$ .

B is ESS<sub>N</sub> if

$$\begin{aligned}
i. \quad b(N-1) &< c+d(N-2) \\
ii. \quad a(N-2) + b(2N-1) &< c(N+1) + d(2N-4) \\
i. \quad 2N-2 &< 17+N-2 \\
N &< 17 \\
ii. \quad 20N-40 + 4N-2 &< 17N+17+2N-4 \\
5N &< 55 \\
N &< 11
\end{aligned}$$

$\therefore B$  is ESS<sub>N</sub> for  $2 \leq N \leq 10$ .

$$1c) (N-2)(a-d) > N(c-b)$$

$$(N-2)(20-1) > N(17-2)$$

$$19N - 38 > 15N$$

$$4N > 38$$

$$N > 9.5$$

$\therefore A$  is risk dominant for  $N \geq 10$ .

### Problem 2: Strong selection

Consider the two-strategy game

$$\begin{array}{cc} & \begin{matrix} A & B \end{matrix} \\ \begin{matrix} A & \end{matrix} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \\ \begin{matrix} B & \end{matrix} & \end{array}$$

- (a) In an *infinite* population with replicator dynamics, decide for all games of this type whether strategies  $A$  and  $B$  are dominant, coexisting, or bi-stable, based on the two variables  $\xi = a - c$  and  $\zeta = d - b$ . **d (1 Point)**

**B**

2a) Let  $\alpha = a - c$ ,  $\beta = d - b$ .

(i)  $A$  dominates  $B$ , if  $a > c$  and  $b > d$ :



$$\rightarrow \alpha > 0, \beta < 0$$

(ii)  $B$  dominates  $A$ , if  $a < c$  and  $b < d$ :



$$\rightarrow \alpha < 0, \beta > 0$$

(iii)  $A$  and  $B$  are bistable, if  $a > c$  and  $b < d$ :



$$\rightarrow \alpha > 0, \beta > 0$$

(iv)  $A$  and  $B$  coexist, if  $a < c$  and  $b > d$ :



$$\rightarrow \alpha < 0, \beta < 0$$

(v)  $A$  and  $B$  are neutral, if  $a = c$  and  $b = d$ :



$$\rightarrow \alpha = 0, \beta = 0$$

Now consider a population of *finite* size  $N$  that evolves according to a unstructured Moran process. Suppose the fitness of  $A$  and  $B$  are given respectively by

$$f_i = \frac{a(i-1) + b(N-i)}{N-1}$$

$$g_i = \frac{ci + d(N-i-1)}{N-1}.$$

Note that this corresponds to limit of strong selection,  $w = 1$ , as compared to the lecture.

We want to classify the evolutionary stability of  $A$  and  $B$  as a function of the population size  $N$  and the payoff values  $a, b, c$ , and  $d$ . To this end we analyze the difference in fitness  $h_i = f_i - g_i$ .

(b) Show that

$$h_i = \xi' \frac{i}{N-1} - \zeta' \frac{N-i}{N-1}$$

with

$$\xi' = \xi - \frac{a-d}{N} \quad \text{and} \quad \zeta' = \zeta + \frac{a-d}{N}.$$

What happens in the limit of large  $N$ ?



(1 Point)

(c) Show that for  $\xi' > 0 > \zeta'$  strategy  $A$  is dominant. Derive a criterion for the dominance of  $B$ .

(1 Point)

(d) Now suppose that  $\xi', \zeta' > 0$ . Show that if  $\frac{1}{N-1} < \xi'/\zeta' < N-1$  it follows  $h_1 < 0 < h_{N-1}$ . Show that  $h_1 < 0 < h_{N-1}$  is a criterion for bi-stability of  $A$  and  $B$ .

Similarly, show that if  $\xi', \zeta' < 0$  and  $\frac{1}{N-1} < \xi'/\zeta' < N-1$  it follows that  $h_1 > 0 > h_{N-1}$ . What does  $h_1 > 0 > h_{N-1}$  imply for the evolutionary stability of  $A$  and  $B$ ? (1 Point)

2b) Show that  $h_i = \underbrace{\left[ (a-c) - \frac{a-d}{N} \right]}_{\alpha} \underbrace{\left( \frac{i}{N-1} \right)}_{A'} - \underbrace{\left[ (d-b) + \frac{a-d}{N} \right]}_{\beta} \underbrace{\left( \frac{N-i}{N-1} \right)}_{B'}$

$$\begin{aligned} h_i &= f_i - g_i = \frac{a(i-1) + b(N-i) - ci + d(N-i-1)}{N-1} & \frac{a-d}{N-1} &= \frac{a-d}{N} \cdot \frac{N}{N-1} \\ &= \frac{ai - a - ci + b(N-i) - d(N-i) + d}{N-1} & &= \frac{a-d}{N} \cdot \frac{i + (N-i)}{N-1} \\ &= \frac{(a-c)i}{N-1} - \frac{(d-b)(N-i)}{N-1} - \frac{a-d}{N-1} & &= \frac{a-d}{N} \left( \frac{i}{N-1} + \frac{N-i}{N-1} \right) \\ &= \frac{i}{N-1} (a-c) - \frac{N-i}{N-1} (d-b) - \frac{a-d}{N-1} \left( \frac{i}{N-1} + \frac{N-i}{N-1} \right) \\ &= \frac{i}{N-1} \left[ (a-c) - \left( \frac{a-d}{N-1} \right) \right] - \frac{N-i}{N-1} \left[ (d-b) \left( \frac{a-d}{N-1} \right) \right] \end{aligned}$$

As  $N \rightarrow \infty$ ,

$$\frac{i}{N-1} \rightarrow 0, \quad \frac{a-d}{N-1} \rightarrow 0, \quad \frac{N-i}{N-1} \rightarrow 1.$$

$$0 \cdot (a-c) - 1 \cdot (d-b) = b-d$$

2c) Let  $\alpha = a - c$ ,  $\beta = d - b$ .

$$\alpha' = \alpha - \frac{a-d}{N}, \quad \beta' = \beta - \frac{a-d}{N}$$

Assume  $\alpha' > 0 > \beta'$ . A dominates if  $a > c$  and  $b > d$

$$\alpha' > 0 \Leftrightarrow \alpha - \frac{a-d}{N} > 0 \Leftrightarrow a - c > \frac{a-d}{N} \quad \text{finite real number} \quad \therefore a - c > 0 \text{ and } a > c.$$

$$\beta' < 0 \Leftrightarrow \beta - \frac{a-d}{N} < 0 \Leftrightarrow d - b < \frac{a-d}{N} \quad \therefore d - b < 0 \text{ and } d < b.$$

$$h_i = f_i - g_i = \underbrace{\alpha' \frac{i}{N-1}}_{>0} - \underbrace{\beta' \frac{N-i}{N-1}}_{<0} > 0$$

$\therefore$  For  $\alpha' > 0 > \beta'$ , A dominates B.

$$2d) \frac{|\alpha'|}{|\beta'|} < N-1 \Leftrightarrow \frac{|\alpha'|}{N-1} < |\beta'| \Leftrightarrow \frac{|\alpha'|}{N-1} - |\beta'| < 0$$

$$\frac{|\alpha'|}{|\beta'|} > \frac{1}{N-1} \Leftrightarrow |\alpha'| > \frac{|\beta'|}{N-1} \Leftrightarrow |\alpha'| - \frac{|\beta'|}{N-1} > 0$$

$$h_{N-1} = |\alpha'| \frac{N-1}{N-1} - |\beta'| \frac{N-(N-1)}{N-1} = |\alpha'| - \frac{|\beta'|}{N-1} > 0$$

$$h_1 = \frac{|\alpha'|}{N-1} - |\beta'| \frac{N-1}{N-1} = \frac{|\alpha'|}{N-1} - |\beta'| < 0$$

$\therefore$  for  $\frac{1}{N-1} < \frac{|\alpha'|}{|\beta'|} < N-1$ ,  $h_1 < 0 < h_{N-1}$  if  $\alpha', \beta' > 0$ .

$h_1 > 0 > h_{N-1}$  if  $\alpha', \beta' < 0$ .

for bi-stability,  $\alpha > 0$  and  $\beta > 0$ . Since  $h_1 < 0 < h_{N-1}$  if  $\alpha, \beta > 0$ , it is a criterion for  $h_1 > 0 > h_{N-1}$  i.e.  $\alpha < 0$  and  $\beta < 0$ , A and B coexist.