

Problem 1: Weak selection

Consider the general two-strategy game

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

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

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

(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.

$$\frac{g_i}{f_i} = \frac{1-w + wg_i}{1-w + wf_i} = \frac{1-w(1-g_i)}{1-w(1-f_i)} \approx 1 - w(f_i - g_i) \text{ for } w \ll 1.$$

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

$$\begin{aligned} f_i - g_i &= \frac{(i-1)a + (N-i)b}{N-1} - \frac{ic + (N-i-1)d}{N-1} = \frac{ia - a + Nb - ib - ic - Nd + id + d}{N-1} \\ &= \frac{i(a-b-c+d) + N(b-d) - a + d}{N-1} \\ &= i \underbrace{\frac{(a-b-c+d)}{N-1}}_x + \underbrace{\frac{N(b-d) - a + d}{N-1}}_y \end{aligned}$$

$$1 + \sum_{k=1}^{N-1} \left[1 - w \sum_{i=1}^k (F_i - G_i) \right] = 1 + \sum_{k=1}^{N-1} 1 - w \sum_{k=1}^{N-1} \sum_{i=1}^k (F_i - G_i)$$

$$= N - w \sum_{k=1}^{N-1} \sum_{i=1}^k (F_i - G_i)$$

$$= N - w \sum_{k=1}^{N-1} \sum_{i=1}^k (ix + y)$$

$$= N - w \left[x \sum_{k=1}^{N-1} \sum_{i=1}^k i + y \sum_{k=1}^{N-1} \sum_{i=1}^k 1 \right]$$

$$= N - w \left[x \frac{(N-1)N(N+1)}{3!} + y \frac{N(N-1)}{2} \right]$$

$$= N - w \left[\frac{(a-b-c+d)}{N-1} \cdot \frac{(N-1)N(N+1)}{6} + \frac{N(b-d)-a+d}{N-1} \cdot \frac{N(N-1)}{2} \right]$$

$$= N - w \left[\frac{(a-b-c+d)N(N+1)}{6} + \frac{N(bN-dN)+N(-a+d)}{2} \right]$$

$$= N - \frac{wN}{6} \left[(a-b-c+d)(N+1) + 3bN - 3dN - 3a + 3d \right]$$

$$= N - \frac{wN}{6} (aN - bN - cN + dN + a - b - c + d + 3bN - 3dN - 3a + 3d)$$

$$= N - \frac{wN}{6} [N(a+2b-c-2d) - (2a+b+c-4d)] = N - \frac{wN}{6} (\alpha N - \beta)$$

$$\therefore P_A = \frac{1}{1 + \sum_{k=1}^{N-1} \prod_{i=1}^k \left(\frac{g_i}{f_i} \right)} = \frac{1}{N - \frac{wN}{6} (\alpha N - \beta)} = \frac{1}{N} \frac{1}{1 - \frac{w}{6} (\alpha N - \beta)}$$

1b) A is ESS_N if

$$i. c(N-1) < b + a(N-2)$$

$$ii. d(N-2) + c(2N-1) < b(N+1) + a(2N-4)$$

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

$$3N > 40 - 2 - 17$$

$$N > 7$$

$$ii. N-2 + 34N - 17 < 2N+2 + 40N-80$$

$$7N > 59$$

$$N > 8.4$$

$\therefore A$ is ESS_N for $N \geq 9$.

B is ESS_N if

$$i. b(N-1) < c+d(N-2)$$

$$ii. a(N-2) + b(2N-1) < c(N+1) + d(2N-4)$$

$$i. 2N-2 < 17 + N-2$$

$$N < 17$$

$$ii. 20N-40 + 4N-2 < 17N+17 + 2N-4$$

$$5N < 55$$

$$N < 11$$

$\therefore B$ is ESS_N 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

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

- (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 $\zeta = d - b$.

α (1 Point)

β

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

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



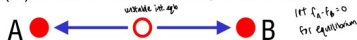
$$\rightarrow \alpha > 0, \beta < 0$$

- (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 an 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 ?

ξ' ζ'

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

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

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

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

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

$$= \frac{i}{N-1} \left[(a-c) - \frac{a-d}{N-1} \right] - \frac{N-i}{N-1} \left[(d-b) - \frac{a-d}{N-1} \right]$$

$$\frac{a-d}{N-1} = \frac{a-d}{N} \cdot \frac{N}{N-1}$$

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

$$= \frac{a-d}{N} \left(\frac{i}{N-1} + \frac{N-i}{N-1} \right)$$

As $N \rightarrow \infty$,

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

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

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

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

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

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

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

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

\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.