Extrapolating Weak Selection in Evolutionary Games

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Abstract

This work is inspired by a 2013 paper from Arne Traulsen's lab at the Max Plank Institute for Evolutionary Biology [10]. They studied the small mutation limit of evolutionary games. It has been shown that for 2×2 games the ranking of the strategies does not change as strength of selection is increased [11]. The point of the 2013 paper is that when there are three or more strategies the ordering can change as selection is increased. Traulsen et al [10] did numerical computations for fixed N. Here, we will instead let the strength of selection $\beta = c/N$ and let $N \to \infty$ to obtain formulas for the invadability probabilities ϕ_{ij} that determine the rankings. The integrals that give these probabilities are difficult to evaluate in general, but they do allow us to compute the ranking order when c is small or c is large. The results we have obtained for five concrete examples lead us to doubt the accuracy of insights that are derived in the small mutation limit for games with three strategies.

1 Introduction

Let a_{ij} be the payoff to a player who uses strategy i against an opponent who uses strategy j. Let x_j be the frequency of strategy j and define the fitness of strategy i to be

$$\psi_i = \sum_j a_{ij} x_j,$$

the payoff when a player with strategy i plays against a randomly chosen individual. We will study how the frequencies behave under *imitation dynamics*. In this evolution a player a chosen at random from the population compares her payoff to an opponent b chosen at random and changes her opinion with probability $g(\beta(\psi_{i(b)} - \psi_{i(a)}))$ where β indicates the strength of selection and $g : \mathbb{R} \to (0,1)$ is a nondecreasing function, such as the Fermi function $g(x) = 1/(1+e^{-x})$. Thinking of biological competition and following in the footsteps

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of [4], Traulsen et al [10] consider the situation is small enough so that at most times there is only one strategy i in the population. In this case a mutation that introduces one j into a population that is all i will go to fixation with probability ϕ_{ij} that can be computed by analyzing a birth and death chain. Having computed ϕ_{ij} one can then analyze the Markov chain with jumps from i to j at rate $\mu\phi_{ij}$ to find the equilibrium frequencies $\pi_i(\beta)$ of the strategies.

The relative sizes of the $\pi_i(\beta)$ gives an ordering of the strategies. It has been shown that for 2×2 games the ranking of the strategies does not change as strength of fitness is increased [11] . The point of [10] is that when there are three or more strategies the ordering can change as β is increased, which the authors tout as a weakness of the "weak selection" viewpoint. In the supplementary materials of [10] they give a complicated argument for the existence of a game in which the strategy ordering can change. In the body of the paper they report on simulations of games with randomly chosen entries that show ranking changes occur in approximately 45% of games.

Here, we will let the strength of selection $\beta = c/N$ and let $N \to \infty$ to obtain formulas for the invadability probabilities ϕ_{ij} that determine the rankings. The integrals that give these probabilities, see (6), are difficult to evaluate in general, but they do allow us to compute the ranking order when c is small or c is large. The dichotomy between small c and large c is similar to that of wN and Nw limits introduced by Jeoeng et al [5] and recently studied by Sample and Allen [8]. In the first case one lets the strength of selection $w \to 0$ the number of individuals $N \to \infty$. In the second the order of the limits is reversed. In our case $w = c?N$ so $w \to 0$ and $N \to \infty$ simultaneously.

The paper is organized as follows: In Section 2 we develop formulas for the ϕ_{ij}. In Section 3 we compute the stationary distribution for the Markov chain that gives the transition between dominant strategies. In Sections 4 and 5 we give our results for small c and large c respectively. Section 6 prepares for the study of examples by developing formulas for the three different classes of 2×2 games. In Sections 7 – 11 we apply our results we have obtained to five concrete examples. As explained in the discussion in Section 12 the results obtained from the small mutation limit lead us to doubt the accuracy of insights that are derived in the small mutation limit. In a nutshell, the method is problematic because it looks only at the 2×2 subgames, and not at whether the third strategy can invade (increase when small), which is the key to the analysis of spatial games in [2] and [7].

2 Formulas for ϕ_{ij}

sec:phi

In what follows we will use a theorem-proof style of exposition to highlight the main results and to allow the reader to skip the details of the derivations For simplicity, we will ignore the fact that you can't play the game against yourself to write the payoffs from playing strategies i and j when k individuals are using strategy j as

$$\psi_i(k) = a_{ii}(N-k)/N + a_{ij}k/N$$
$$\psi_j(k) = a_{ji}(N-k)/N + a_{jj}k/N$$

Here, i is the wild type, j is the mutant. The payoff difference $\Delta_{ji}(k) = \psi_j(k) - \psi_i(k)$ is

$$= \frac{(a_{ji} - a_{ii})(N-k) + (a_{jj} - a_{ij})k}{N}$$
$$= (a_{ji} - a_{ii}) + (a_{ii} - a_{ji} - a_{ij} + a_{jj})\frac{k}{N}$$

Note that if we add c_k to the entries in the kth column, the payoff difference is not changed so we can without loss of generality suppose that the diagonal entries are 0. If we do this then the payoff difference is

$$= a_{ji} - (a_{ji} + a_{ij})\frac{k}{N} \tag{1}$$ paydiff

We assume that each individual updates his strategy at rate 1, so the jump rates

$$p(k, k+1) = (N-k) \cdot \frac{k}{N} g(\beta \Delta_{ji}(k))$$
$$p(k, k-1) = k \cdot \frac{N-k}{N} g(-\beta \Delta_{ji}(k))$$

Our first step is to compute the fixation probability. The next result is the same as (4) in the supplementary materials of [10]. In hte context of evoluitonary games this formula was derived by Taylor et al [9]. However it was first discovered by Karlin and McGregor in the late 1950s [6].

Theorem 1. *If* $T_k = \min\{t : X_t = k\}$ *then we have*

$$P_1(T_N < T_0) = \frac{1}{\sum_{k=1}^N \prod_{\ell=1}^{k-1} \frac{p(\ell,\ell-1)}{p(\ell,\ell+1)}} \tag{2}$$ jinvi

Proof. The first step is to define a function that has $h(0) = 0$, $h(1) = 1$, and

$$h(k) = p(k, k+1)h(k+1) + p(k, k-1)h(k-1). \tag{3}$$ hrec

The last equation implies that if we let X_t be the number of the invading type at time t, then $E_x h(X_t)$ remains constant so

$$P_1(T_N < T_0) = \frac{1}{h(N)} \tag{4}$$ hitpr

To find h we note that (3) implies

$$h(k+1) - h(k) = \frac{p(k, k-1)}{p(k, k+1)}(h(k) - h(k-1))$$

Iterating and using $h(1) - h(0) = 1$ it follows that

$$h(k) - h(k-1) = \prod_{\ell=1}^{k-1} \frac{p(\ell, \ell-1)}{p(\ell, \ell+1)}$$

and hence

$$h(m) = \sum_{k=1}^{m} \prod_{\ell=1}^{k-1} \frac{p(\ell, \ell-1)}{p(\ell, \ell+1)} \tag{5}$$ hformula

so using (4) gives (2). □

Theorem 2. *If we let $\gamma = g'(0)/g(0)$ and suppose $N\beta \to c$ then $\phi_{ij} \approx 1/NI_{ij}$ where*

$$I_{ij} = \frac{1}{N\int_0^1 \exp\left(-2\gamma c[a_{ji}x - (a_{ji}+a_{ij})x^2/2]\right)\,dx} \tag{6}$$ phiij

Note that the answer only depends on $2\gamma c$ so we can without loss of generality suppose $\gamma = 1/2$. Here and in what follows we will write our results as approximations rather than asymptotic formulas so hhtat we do not have to estimate the size of errors

Proof. To begin to understand (2) we look at the ratio

$$\begin{aligned}\frac{p(\ell,\ell-1)}{p(\ell,\ell+1)} &= \frac{g(-\beta\Delta_{ji}(k))}{g(\beta\Delta_{ji}(\ell))} \approx \frac{g(0)-g'(0)\beta\Delta_{ji}(k)}{g(0)+g'(0)\beta\Delta_{ji}(\ell)}\\ &\approx 1 - 2\gamma\beta\Delta_{ji}(\ell) = 1 - 2\gamma\beta[a_{ji} - (a_{ji}+a_{ij})(\ell/N)]\end{aligned}$$

Note that γ is the only aspect of g relevant to the value of ϕ_{ij}. For the Fermi function $g(x) = 1/(1+e^{-x})$, $g'(x) = e^{-x}/(1+e^{-x})^2$ so $\gamma = 1/4$.

$$\prod_{\ell=1}^{k-1}\frac{p(\ell,\ell-1)}{p(\ell,\ell+1)} \approx \prod_{\ell=1}^{k-1} 1 - 2\gamma\beta\Delta_{ji}(\ell)$$

Taking log and using $\log(1-x) \approx -x$ we have

$$\begin{aligned}\log\prod_{\ell=1}^{k-1}\frac{p(\ell,\ell-1)}{p(\ell,\ell+1)} &\approx -\sum_{\ell=1}^{k-1} 2\gamma\beta[a_{ji} - (a_{ji}+a_{ij})(\ell/N)]\\ &\approx -2\gamma\beta[a_{ji}k - (a_{ji}+a_{ij})(k^2/2N)]\end{aligned}$$

so we have

$$\prod_{\ell=1}^{k-1}\frac{p(\ell,\ell-1)}{p(\ell,\ell+1)} \approx \exp\left(-2\gamma\beta[a_{ji}k - (a_{ji}+a_{ij})(k^2/2N)]\right)$$

and it follows that if $\beta N \to c$

$$\begin{aligned}\frac{1}{N}\sum_{k=1}^{N}\prod_{\ell=1}^{k-1}\frac{p(\ell,\ell+1)}{p(\ell,\ell-1)} &\approx \int_0^1 \exp\left(-2\gamma\beta N[a_{ji}x - (a_{ji}+a_{ij})x^2/2]\right)\,dx\\ &\to \int_0^1 \exp\left(-2\gamma c[a_{ji}x - (a_{ji}+a_{ij})x^2/2]\right)\,dx\end{aligned} \tag{7}$$ limofh

which proves the desired result. □

3 Equilibrium distribution

sec:eq

If μ is the mutation rate from i to $j \neq i$ the transition rate matrix is

$$\begin{pmatrix} -\mu(\phi_{12}+\phi_{13}) & \mu\phi_{12} & \mu\phi_{13}\\ \mu\phi_{21} & -\mu(\phi_{21}+\phi_{23}) & \mu\phi_{23}\\ \mu\phi_{31} & \mu\phi_{32} & -\mu(\phi_{31}+\phi_{32})\end{pmatrix}$$

To find the stationary distribution, we need to solve

$$\begin{pmatrix}\pi_1 & \pi_2 & \pi_3\end{pmatrix}\begin{pmatrix}-\mu(\phi_{12}+\phi_{13}) & \mu\phi_{12} & 1\\ \mu\phi_{21} & -\mu(\phi_{21}+\phi_{23}) & 1\\ \mu\phi_{31} & \mu\phi_{32} & 1\end{pmatrix} = \begin{pmatrix}0 & 0 & 1\end{pmatrix} \tag{8}$$

pieqn

The solution is straightforward, but somewhat tedious, so we just give the answer:

$$\begin{aligned}\pi_1 &= (\phi_{31}\phi_{21}+\phi_{32}\phi_{21}+\phi_{23}\phi_{31})/D\\ \pi_2 &= (\phi_{12}\phi_{32}+\phi_{13}\phi_{32}+\phi_{31}\phi_{12})/D\\ \pi_3 &= (\phi_{23}\phi_{13}+\phi_{21}\phi_{13}+\phi_{12}\phi_{23})/D\end{aligned} \tag{9}$$

pieq

where D is the sum of the three numerators. The three formulas can be collapsed into one by writing

$$\pi_i = (\phi_{ji}\phi_{ki}+\phi_{jk}\phi_{ki}+\phi_{kj}\phi_{ji})/D$$

where $j = i-1$ and $k = i+1$ and the arithmetic is done in $\mathbb{Z} \bmod 3 = \{1,2,3\}$.

4 Small c

sec:smallc

The main result of this section is (11) which allows us to compute the strategy ranking for small c. The reader who gets bored with the details can skip to that point. If c is small

$$\begin{aligned}I_{i,j} &\equiv \int_0^1 \exp\left(-c[a_{ji}x-(a_{ji}+a_{ij})x^2/2]\right)\,dx\\ &\approx \int_0^1 1-c[a_{ji}x-(a_{ji}+a_{ij})x^2/2]\,dx = 1-c[a_{ji}/2-(a_{ji}+a_{1j})/6]\end{aligned}$$

so using (6)

$$\phi_{ij} \approx \frac{1}{N}(1+c\psi_{ij}) \quad \text{where} \quad \psi_{ij} = \frac{a_{ji}}{2} - \frac{a_{ji}+a_{ij}}{6}$$

If we (i) cancel the $1/N$'s and then drop terms of order c^2 then the numerators n_i of the π_i are

$$\begin{aligned}n_1 &= 3+c[\psi_{31}+\psi_{21}+\psi_{23}+\psi_{31}+\psi_{32}+\psi_{21}]\\ n_2 &= 3+c[\psi_{32}+\psi_{12}+\psi_{31}+\psi_{12}+\psi_{13}+\psi_{32}]\\ n_3 &= 3+c[\psi_{13}+\psi_{23}+\psi_{21}+\psi_{13}+\psi_{12}+\psi_{23}]\end{aligned}$$

Note that

in	are missing	appear twice
n_1	1,2 and 1,3	3,1 and 2,1
n_2	2,1 and 2,3	3,2 and 1,2
n_3	3,2 and 3,1	1,3 and 2,3

If we let $\Gamma = 3 + c[\psi_{12} + \psi_{13} + \psi_{21} + \psi_{23} + \psi_{31} + \psi_{32}]$ then

$$\begin{aligned} n_1 &= \Gamma - c[\psi_{12} - \psi_{21} + \psi_{13} - \psi_{31}] \\ n_2 &= \Gamma - c[\psi_{21} - \psi_{12} + \psi_{23} - \psi_{32}] \\ n_3 &= \Gamma - c[\psi_{32} - \psi_{23} + \psi_{31} - \psi_{13}] \end{aligned}$$

To check the arithmetic, note that the terms that are missing must be positive inside the square brackets while those that appear twice must be negative.

The relative sizes of the n_i gives the strategy ordering for small c. To further simplify we note that $\psi_{ij} - \psi_{ji} = (a_{ji} - a_{ij})/2$. so if we let

$$d_{ij} = (a_{ji} - a_{ij})/2 \tag{10}$$ dij

and note that $d_{ji} = -d_{ij}$ then we have

$$\begin{aligned} n_1 &= \Gamma - c[d_{12} - d_{31}] \\ n_2 &= \Gamma - c[d_{23} - d_{12}] \\ n_3 &= \Gamma - c[d_{31} - d_{23}] \end{aligned} \tag{11}$$ nis

We have used d_{31} instead of d_{13} so we have the general formula

$$n_i = \Gamma - c[d_{i,i+1} - d_{i-1,i}]$$

where the arithmetic is done modulo 3. It is not easy to write a formula for the ranking in terms of the entries of the game matrix. However, as the reader will see when we consider examples, it is easy to compute the rankings for a given example.

5 Large c

sec:largec

The main result of the section is given in the table at the end. The reader who gets bored by the calculus can skip to that point. We are interested in estimating the size of

$$I_{ij} = \int_0^1 \exp\left(-c[a_{ji}x - (a_{ji} + a_{ij})x^2/2]\right)\, dx$$

when c is large. This will be determined by the largest value of the integrand on $[0, 1]$. To simplify notation we let $\alpha = -a_{ji}$, let $\beta = a_{ji} + a_{ij}$, and Artie

$$I = \int_0^1 \exp(ch(x))\, dx \quad \text{where} \quad h(x) = \alpha x + \beta x^2/2$$

We begin with the case $\beta = 0$. If $\alpha < 0$

$$I \approx \int_0^\epsilon \exp(c\alpha x)\, dx \approx 1/(-\alpha c) \tag{12}$$ b0aneg

If $\alpha > 0$ we change variables $x = 1 - y$

$$I \approx \int_0^\epsilon \exp(c\alpha(1 - y))\, dx \approx \exp(\alpha c)/(\alpha c) \tag{13}$$ b0apos

Suppose now $\beta \neq 0$. Taking the derivative $h'(x) = \alpha + \beta x$ so $h'(x) = 0$ at $x^* = -\alpha/\beta$. There are several cases for the location of the maximum of the integrand

	$\beta > 0$	$\beta < 0$
$x^* \le 0$	1	0
$x^* \ge 1$	0	1
$0 < x^* \le 1/2$	1	x^*
$1/2 \le x^* < 1$	0	x^*

If the maximum occurs at 0 then $h'(0) = \alpha < 0$ and

$$I \approx \int_0^\epsilon \exp(c\alpha x)\,dx \approx 1/(-c\alpha). \tag{14}$$ max0

If the maximum occurs at 1 then we change variables $x = 1 - y$ to get

$$\begin{aligned} I &\approx \int_0^\epsilon \exp(c[\alpha(1-y) + \beta(1-y)^2/2])\,dy \\ &\approx \exp(c(\alpha + \beta/2)) \int_0^\epsilon \exp(-c[(\alpha+\beta)y])\,dy \\ &\approx \exp(c(\alpha+\beta/2)) \cdot \frac{1}{c(\alpha+\beta)} \end{aligned} \tag{15}$$ max1

Note that if the maximum occurs at 1 then $\alpha + \beta > 0$. If $\beta < 0$ then $\alpha + \beta/2 > \alpha + \beta > 0$. If $\beta > 0$ then we are only in this case when $x^* = -\alpha/\beta \le 1/2$ so $\alpha + \beta/2 \ge 0$.

If the maximum occurs at $x^* = -\alpha/\beta \in (0,1)$ then from the table we see that $\beta < 0$ and $0 < \alpha < -\beta$. We change variables $y = x - x^*$

$$\begin{aligned} I &\approx \int_{-\epsilon}^\epsilon \exp(c[\alpha(y+x^*) + \beta(y+x^*)^2/2])\,dy \\ &\approx \int_{-\epsilon}^\epsilon \exp\left(c\left[\alpha y - \alpha^2/\beta + \frac{\beta}{2}\left(y^2/2 - 2y\alpha/\beta + (-\alpha/\beta)^2\right)\right]\right)\,dy \\ &= \exp(-c\alpha^2/2\beta) \int_{-\epsilon}^\epsilon \exp(c\beta y^2/2)\,dy \end{aligned}$$

The second and fifth terms combine to produce the one out front. The first and fourth cancel. Recalling that normal(0,σ^2) density is $(2\pi\sigma^2)^{-1/2}\exp(-y^2/2\sigma^2)$ and taking $\sigma^2 = 1/(-c\beta)$ we see that

$$I \approx (2\pi/(-c\beta))^{1/2}\exp(-c\alpha^2/2\beta) \tag{16}$$ maxint

Combining the table that gives the location of the maxima with the last five calculations.

6 Three types of edges

sec:threee

To prepare for using the large c formulas on examples, we note that I_{ij} and I_{ji} only depend on the 2×2 subgame with strategies i and j. In this game only three things can happen $i \gg j$, there is a stable mixed strategy equilibrium, or there is an unstable mixed strategy equilibrium

Case 1. i dominates j. Since we have 0's on the diagonal $a_{ij} > 0$ and $a_{ij} < 0$. We can have $\beta = a_{ij} + a_{ji}$ positive or negative.

case	condition	max	I
I	$\beta > 0$, $x^* \geq 1/2$ or $\beta < 0$, $x^* \leq 0$	0	$1/(-c\alpha)$
II	$\beta > 0$, $x^* \leq 1/2$ or $\beta < 0$, $x^* \geq 1$	1	$\exp(c(\alpha + \beta/2))/c(\alpha + \beta)$
III	$\beta < 0$, $0 < x^* < 1$,	$x^* = -\alpha/\beta$	$\exp(-c\alpha^2/2\beta) \cdot (2\pi/(-c\beta))^{1/2}$
IV	$\beta = 0$, $\alpha < 0$	0	$1/(-c\alpha)$
V	$\beta = 0$, $\alpha > 0$	1	$\exp(c\alpha)/(c\alpha)$

Table 1: Formulas for large c

$$\begin{array}{llll} \beta > 0 & I_{ij} & \alpha = -a_{ji} > 0 & x^*_{ij} = -\alpha/\beta < 0 & \text{II} \\ & I_{ji} & \alpha = -a_{ij} < 0 & x^*_{ji} = -\alpha/\beta > 1 & \text{I} \\ \beta < 0 & I_{ij} & \alpha = -a_{ji} > 0 & x^*_{ij} = -\alpha/\beta > 1 & \text{II} \\ & I_{ji} & \alpha = -a_{ij} < 0 & x^*_{ij} = -\alpha/\beta < 0 & \text{I} \end{array}$$

Thus in either case $I_{ij} = \exp(c(\alpha + \beta/2))/c(\alpha + \beta)$ and $I_{ji} = 1/(-c\alpha)$.

Case 2. Stable mixed strategy equilibrium. $a_{ij} > 0$ and $a_{ji} > 0$. Suppose without loss of generality that $\rho_i = a_{ij}/(a_{ij} + a_{ji}) < 1/2$

$$\begin{array}{llll} I_{ij} & \alpha = -a_{ji} < 0 & x^* = -\alpha/\beta = 1 - \rho_i > 1/2 & \text{I} \\ I_{ji} & \alpha = -a_{ij} < 0 & x^* = -\alpha/\beta = \rho_i < 1/2 & \text{II} \end{array}$$

Note that when i has $\rho_i < 1/2$, I_{ji} is large.

Case 3. Unstable mixed strategy. $a_{ij} < 0$ and $a_{ji} < 0$. In either case

$$I_{ij} = (2\pi/(-c\beta))^{1/2} \exp(-c\alpha^2/2\beta)$$

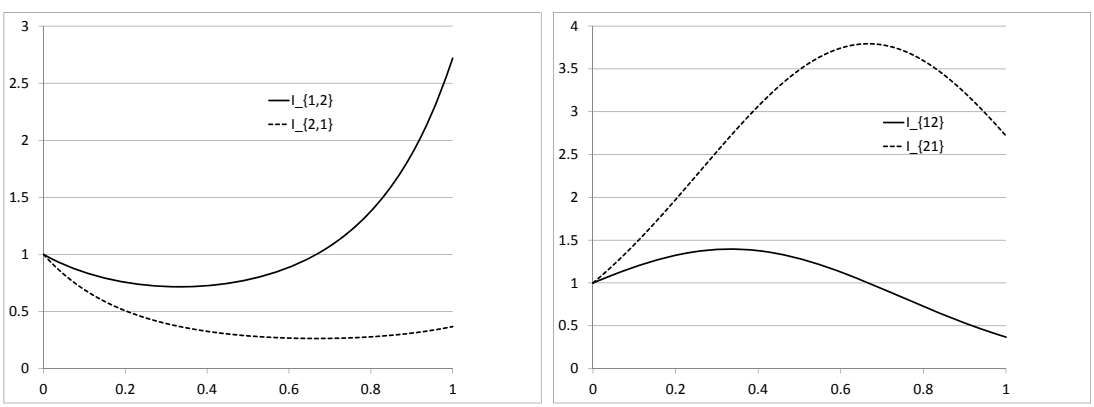


Figure 1: Left: The integrands of I_{12} and I_{21} when $a_{21} = 4$ and $a_{12} = 2$ (case 2, left) and when $a_{21} = -4$ and $a_{12} = -2$ (case 3, right). fig:Iij2

7 Example 1. Rock-paper-scissors

sec:RPS

The game matrix is

	1	**2**	**3**
1	0	1	−2
2	−3	0	2
3	4	−1	0

Writing $i \gg j$ for strategy i dominates strategy j in the (i, j) subgame this example has $1 \gg 2 \gg 3 \gg 1$, which is the same as strategy relationship in the rock-paper-scissors game.

Small c. Using (10) and (11)

$$\begin{aligned} d_{12} &= (a_{21} - a_{12})/2 = -2 \\ d_{23} &= (a_{32} - a_{23})/2 = -1.5 \\ d_{31} &= (a_{13} - a_{31})/2 = -3 \end{aligned}$$

so we have $d_{12} - d_{31} = 1$, $d_{23} - d_{12} = 0.5$, $d_{31} - d_{23} = -1.5$ and it follows that

$$n_1 = \Gamma - c \qquad n_2 = \Gamma - c/2 \qquad n_3 = \Gamma + 1.5c$$

Noting that $n_3 > n_2 > n_1$, we see that for small c, $3 > 2 > 1$.

Large c. To use the formulas derived in Sections 5 and 6 we compute $\alpha = -a_{ji}$, $\beta = (a_{ji} + a_{ij})$, and $x^* = -\alpha/\beta$.

i, j	α	β	x^*	case	$I_{i,j}$
12	3	−2	1.5	II	$\exp(2c)/c$
21	−1	−2	−0.5	I	$1/c$
13	−4	2	2	I	$1/4c$
31	2	2	−1	II	$\exp(3c)/4c$
23	1	1	−1	II	$\exp(3c/2)/2c$
32	−2	1	2	I	$1/2c$

If we recall that (6) implies $\phi_{ij} \approx 1/NI_{ij}$, i.e., a large I_{ij} means that it is very difficult for j to invade i, then we see that the answers consistent with the ordering $1 \gg 2 \gg 3 \gg 1$: ϕ_{12}, ϕ_{23}, and ϕ_{31} are exponentially small. When we use (9) the N's cancel out. Marking the small terms with *'s

$$\begin{aligned} D\pi_1 &= \phi^*_{31}\phi_{21} + \phi_{32}\phi_{21} + \phi^*_{23}\phi^*_{31} \approx 2c^2 \\ D\pi_2 &= \phi^*_{12}\phi_{32} + \phi_{13}\phi_{32} + \phi^*_{31}\phi^*_{12} \approx 8c^2 \\ D\pi_3 &= \phi^*_{23}\phi_{13} + \phi_{21}\phi_{13} + \phi^*_{12}\phi^*_{23} \approx 4c^2 \end{aligned}$$

so for large c we have $2 > 3 > 1$, a change from the small c ranking of $3 > 2 > 1$.

Generalizing from the concrete example we see that if $1 \gg 2 \gg 3 \gg 1$ then all the $d_{i,i+1}$ are negative. If d_{31} is the smallest then

$$d_{31} - d_{23} < 0 < d_{12} - d_{31}$$

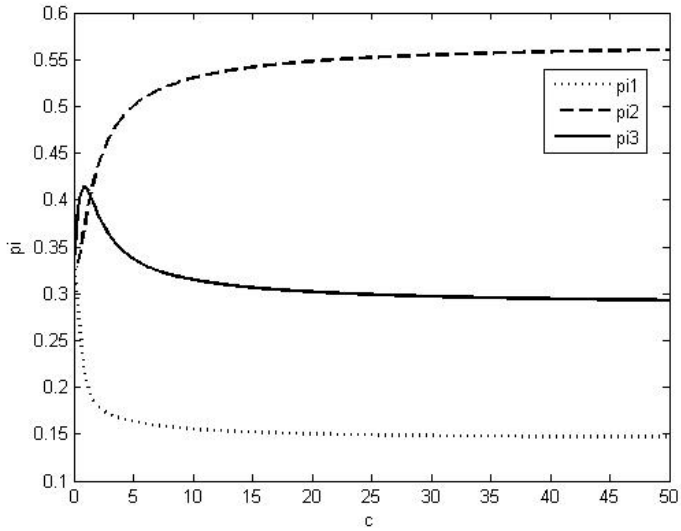


Figure 2: Strategy rankings for Example 1. The ranking changes from $3 > 2 > 1$ to $2 > 3 > 1$ when $c \approx 2$. fig:ex1

but $d_{23} - d_{12}$ could be smallest, largest, or in the middle. If $i \gg j$ then $N\phi_{ji} \approx a_{ij}c$ so we have

$$D\pi_1 = a_{23}a_{12}c^2 \quad D\pi_2 = a_{31}a_{23}c^2 \quad D\pi_3 = a_{12}a_{31}c^2 \tag{17}$$ RPSasy

Since the small c rankings are based on a linear function of the matrix entries and the large c formulas are quadratic, it is not surprising that they can be different.

The asymptotic formula in (17) implies

$$D \sim [a_{23}a_{12} + a_{31}a_{23} + a_{12}a_{31}]c^2$$

In the concrete example this implies

$$\pi_1 \to 1/7, \qquad \pi_2 \to 4/7, \qquad \pi_3 \to 2/7,$$

which agrees with Figure 2.

8 Example 2. One stable edge fixed point

sec:ex2

The game matrix is

	1	**2**	**3**
1	0	2	-1
2	4	0	3
3	2	-2	0

The 1,2 subgame has a mixed strategy equilibrium $(1/3, 2/3)$ in which each strategy has fitness $4/3$. When played against this equilibrium 3 has fitness $2/3 - 4/3 = -2/3$ so it cannot invade. In the other 2×2 subgames $3 \gg 1$ and $2 \gg 3$.

Small c. Using (10) and (11)

$$\begin{aligned} d_{12} &= (a_{21} - a_{12})/2 = (4-2)/2 = 1 \\ d_{23} &= (a_{32} - a_{23})/2 = (-2-3)/2 = -2.5 \\ d_{31} &= (a_{13} - a_{31})/2 = (-1-2)/2 = -1.5 \end{aligned}$$

so we have $d_{12} - d_{3,1} = 2.5$, $d_{23} - d_{12} = -3.5$ and $d_{31} - d_{23} = 1$ and it follows that

$$n_1 = \Gamma - 2.5c \qquad n_2 = \Gamma + 3.5c \qquad n_3 = \Gamma - c$$

Noting that $n_2 > n_3 > n_1$, we see that for small c, $2 > 3 > 1$.

Large c. Again we need to compute $\alpha = -a_{ji}$, $\beta = (a_{ji} + a_{ij})$, and $x^* = -\alpha/\beta$.

i,j	α	β	x^*	case	I_{ij}
12	-4	6	2/3	I	$1/4c$
21	-2	6	1/3	II	$\exp(c)/4c$
13	-2	1	2	I	$1/2c$
31	1	1	-1	II	$\exp(3c/2)/2c$
23	2	1	-2	II	$\exp(5c/2)/3c$
32	-3	1	3	I	$1/3c$

Again (6) implies $\phi_{ij} = 1/NI_{ij}$, so ϕ_{21}, ϕ_{31} and ϕ_{23} are exponentially small. Consulting the formula for the stationary distribution and marking the small terms with *

$$\begin{aligned} D\pi_1 &= \phi^*_{31}\phi^*_{21} + \phi_{32}\phi^*_{21} + \phi^*_{23}\phi^*_{31} \\ D\pi_2 &= \phi_{12}\phi_{32} + \phi_{13}\phi_{32} + \phi^*_{31}\phi_{12} \\ D\pi_3 &= \phi^*_{23}\phi_{13} + \phi^*_{21}\phi_{13} + \phi_{12}\phi^*_{23} \end{aligned}$$

From this we see that $D\pi_2 \approx 3c \cdot 4c + 0 + 2c \cdot 3c = 18c^2$ while π_1 and π_3 are exponentially small. To compare π_1 and π_3 we need to compute the exact order of the three terms.

$D\pi_1$	1.5	1	0	1	2.5	1.5
$D\pi_3$	2.5	0	1	0	0	2.5

so we have $D\pi_1 \approx 12c^2 \exp(-c)$ and $D\pi_3 \approx 8c^2 \exp(-c)$. Thus for large c we have $2 > 1 > 3$. π_1 and π_3 are both exponentially small so $\pi_2 \to 1$.

9 Example 3. Two stable edge fixed points

sec:ex3

The game matrix is

	1	**2**	**3**
1	0	1	-1
2	2	0	3
3	2	1	0

The 1,2 subgame has a mixed strategy equilibrium $(1/3, 2/3)$ in which each strategy has fitness 2/3. When played against this equilibrium, strategy 3 has fitness $2/3 + 2/3 = 4/3$

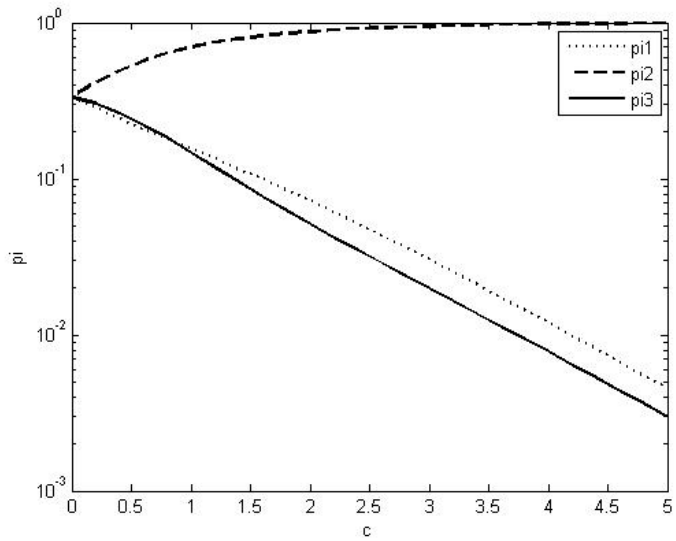


Figure 3: Strategy rankings for Example 2 as a function of c. Frequencies are plotted on a log scale so that we can see π_1 and π_3 have the same exponential decay rate but π_1 has a larger constant. fig:ex2log

so it can invade. The 2,3 subgame has a mixed strategy equilibrium $(3/4, 1/4)$ in which each strategy has fitness 3/4. When played against this equilibrium, strategy 1 has fitness $3/4 - 1/4 = 1/2$ so 1 cannot invade. In the 1,3 subgame $3 \gg 1$

Small c. Using (10) and (11)

$$\begin{aligned} d_{12} &= (a_{21} - a_{12})/2 = (2-1)/2 = 0.5 \\ d_{23} &= (a_{32} - a_{23})/2 = (1-3)/2 = -1 \\ d_{31} &= (a_{13} - a_{31})/2 = (-1-2)/2 = -1.5 \end{aligned}$$

so we have

$$\begin{aligned} d_{12} - d_{3,1} &= 0.5 - (-1.5) = 2 \\ d_{23} - d_{12} &= -1 - 0.5 = -1.5 \\ d_{31} - d_{23} &= -1.5 - (-1) = -0.5 \end{aligned}$$

and it follows from (11) that

$$n_1 = \Gamma - 2c \qquad n_2 = \Gamma + 3c/2 \qquad n_3 = \Gamma + c/2$$

Noting that $n_2 > n_3 > n_1$, we see that for small c, $2 > 3 > 1$.

Large c. Again, $\alpha = -a_{ji}$, $\beta = (a_{ji} + a_{ij})$, and $x^* = -\alpha/\beta$.

i,j	α	β	x^*	case	I
12	-2	3	$2/3$	I	$1/2c$
21	-1	3	$1/3$	II	$\exp(c/2)/2c$
13	-2	1	2	I	$1/2c$
31	1	1	-1	II	$\exp(3c/2)/2c$
23	-1	4	$1/4$	II	$\exp(c)/3c$
32	-3	4	$3/4$	I	$1/3c$

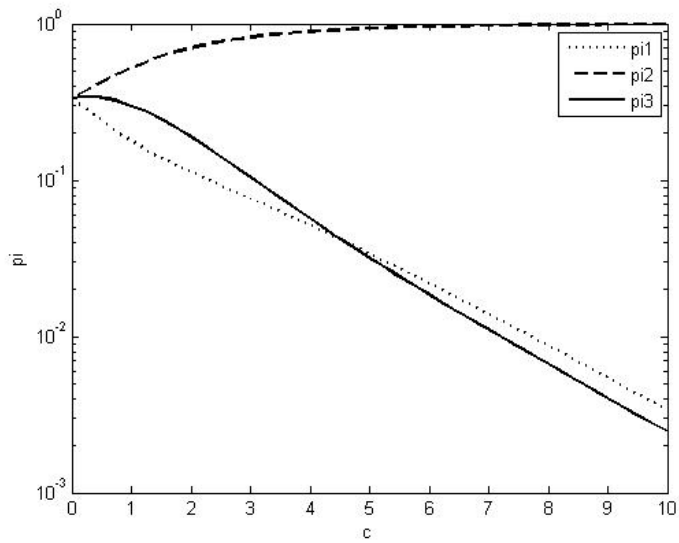


Figure 4: Strategy rankings in Example 3 as a function of c. Again the exponential decay rates are the same in π_1 and π_3. fig:ex3log

Using (6), $\phi_{ij} = 1/NI_{ij}$ we see that again ϕ_{21}, ϕ_{31} and ϕ_{23} are exponentially small, so marking the small terms with *'s, we have the same pattern as in the previous example.

$$\begin{aligned} D\pi_1 &= \phi^*_{31}\phi^*_{21} + \phi_{32}\phi^*_{21} + \phi^*_{23}\phi^*_{31} \\ D\pi_2 &= \phi_{12}\phi_{32} + \phi_{13}\phi_{32} + \phi^*_{31}\phi_{12} \\ D\pi_3 &= \phi^*_{23}\phi_{13} + \phi^*_{21}\phi_{13} + \phi_{12}\phi^*_{23} \end{aligned}$$

From this we see that

$$D\pi_2 \approx 2c \cdot 3c + 2c \cdot 3c = 12c^2.$$

while π_1 and π_3 are exponentially small. To compare π_1 and π_3 we need to compute the exact order of the three terms.

$D\pi_1$	1.5	0.5	0	0.5	1	1.5
$D\pi_3$	1	0	0.5	0	0	1

so we have $D\pi_1 \approx 6c^2\exp(-c/2)$ and $D\pi_3 \approx 4c^2\exp(-c/2)$. Thus for large c we have $2 > 1 > 3$. π_1 and π_3 are both exponentially small so $\pi_2 \to 1$.

10 Example 4. One stable, one unstable

sec:ex4

The game matrix is

	1	**2**	**3**
1	0	2	-1
2	4	0	-3
3	2	-1	0

The 1,2 subgame has a mixed strategy equilibrium $(1/3, 2/3)$ in which each strategy has fitness 4/3. When played against this equilibrium 3 has fitness $2/3 - 2/3 = 0$ so it cannot invade. The 2,3 subgame has an unstable mixed strategy equilibrium $(3/4, 1/4)$ which can be invaded by 1. In the 1,3 subgame $3 \gg 1$.

Small c. Using (10) and (11)

$$\begin{aligned} d_{12} &= (a_{21} - a_{12})/2 = (4-2)/2 = 1 \\ d_{23} &= (a_{32} - a_{23})/2 = (-1-(-3))/2 = 1 \\ d_{31} &= (a_{13} - a_{31})/2 = (-1-2)/2 = -1.5 \end{aligned}$$

so we have

$$\begin{aligned} d_{12} - d_{3,1} &= 1 - (-1.5) = 2.5 \\ d_{23} - d_{12} &= 1 - 1 = 0 \\ d_{31} - d_{23} &= -1.5 - 1 = -2.5 \end{aligned}$$

and it follows that

$$n_1 = \Gamma - 5c/2 \qquad n_2 = \Gamma \qquad n_3 = \Gamma + 5c/2$$

Noting that $n_3 > n_2 > n_1$, we see that for small c, $3 > 2 > 1$.

Large c. Again, $\alpha = -a_{ji}$, $\beta = (a_{ji} + a_{ij})$, and $x^* = -\alpha/\beta$. We have an instance of case III here. In this case $I_{ij} = \exp(-\alpha^2 c/(2\beta))/Ac^{1/2})$ where $A = (-\beta/2\pi)^{1/2} = 0.7979$

i,j	α	β	x^*	case	I
12	-4	6	2/3	I	$1/4c$
21	-2	6	1/3	II	$\exp(c)/4c$
13	-2	1	2	I	$1/2c$
31	1	1	-1	II	$\exp(3c/2)/2c$
23	1	-4	1/4	III	$\exp(c/8)/Ac^{1/2}$
32	3	-4	3/4	III	$\exp(9c/8)/Ac^{1/2}$

Using (6), $\phi_{ij} = 1/NI_{ij}$ we see that again ϕ_{21}, ϕ_{31}, ϕ_{23}, and $\phi_{3,2}$ are exponentially small, so marking the small terms with *'s, we have

$$\begin{aligned} D\pi_1 &= \phi^*_{31}\phi^*_{21} + \phi^*_{32}\phi^*_{21} + \phi^*_{23}\phi^*_{31} \\ D\pi_2 &= \phi_{12}\phi^*_{32} + \phi_{13}\phi^*_{32} + \phi^*_{31}\phi_{12} \\ D\pi_3 &= \phi^*_{23}\phi_{13} + \phi^*_{21}\phi_{13} + \phi_{12}\phi^*_{23} \end{aligned}$$

This time all three terms are exponentially small. The exponential orders of the terms are

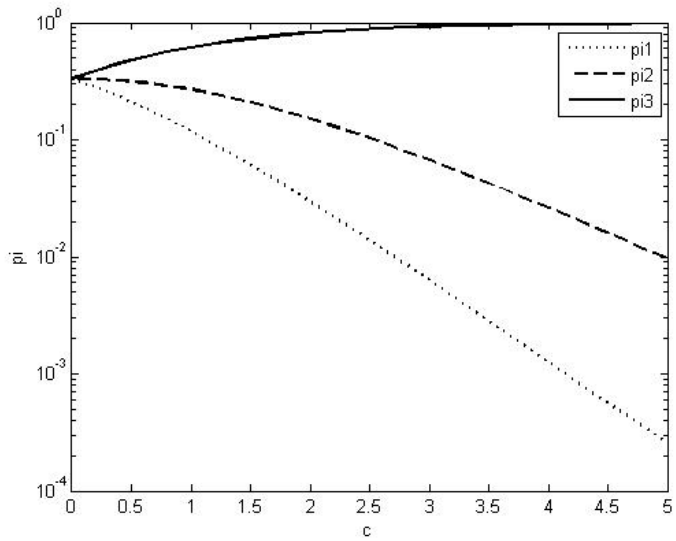


Figure 5: In Example 4 the strategy ranking $3 > 2 > 1$ does not change. As $c \to \infty$, $\pi_3 \to 1$ exponentially fast. In contrast to the two previous examples the exponential decay rates for π_1 and π_2 are different. fig:ex4log

$D\pi_1$	1.5	1	1.125	1	0.125	1.5
$D\pi_2$	0	1.125	0	1.125	1.5	0
$D\pi_3$	0.125	0	1	0	0	0.125

so we have

$$D\pi_1 \approx 2Ac^{3/2}e^{-1.625} \qquad D\pi_2 \approx 6Ac^{3/2}e^{-1.1.25} \qquad D\pi_3 \approx 6Ac^{3/2}e^{-0.125}$$

This the ranking remains the same for large c: $3 > 2 > 1$.

11 Example 5. Two ranking changes

sec:ex5

In the previous four examples there has been a most one ranking change. We now give an example with two changes. The game matrix is

	1	**2**	**3**
1	0	3.2	3.1
2	−1.2	0	2.4
3	5.7	−4.8	0

The 1,3 subgame has a mixed strategy equilibrium (3.1/8.8,5.7/8.8) in which each strategy has fitness $(5.7)(3.1/8.8) = 2.008$. When played against this equilibrium 2 has fitness $[(-1.2)(3.1) + (2.4)(5.7)]/8.8 = 1.13$, so 2 cannot invade. In the other two 2×2 subgames $1 \gg 2$ and $2 \gg 3$.

Small c. Using (10) and (11)

$$d_{12} = (a_{21} - a_{12})/2 = -2.2$$
$$d_{23} = (a_{32} - a_{23})/2 = -3.6$$
$$d_{31} = (a_{13} - a_{31})/2 = -1.3$$

so we have

$$d_{12} - d_{31} = -2.2 - (-1.3) = -0.9$$
$$d_{23} - d_{12} = -3.6 - (-2.2) = -1.4$$
$$d_{31} - d_{23} = -1.3 - (-3.6) = 2.3$$

and it follows that

$$n_1 = \Gamma + 0.9c \qquad n_2 = \Gamma + 1.4c \qquad n_3 = \Gamma - 2.3c$$

Noting that $n_2 > n_1 > n_3$, we see that for small c, $2 > 1 > 3$.

Large c. Again, $\alpha = -a_{ji}$, $\beta = (a_{ji} + a_{ij})$, and $x^* = -\alpha/\beta$.

i, j	α	β	x^*	case	I
12	1.2	2	−0.6	II	$\exp(2.2c)/(3.2c)$
21	−3.2	2	1.6	I	$1/3.2c$
13	−5.7	8.8	0.6477	I	$1/5.7c$
31	−3.1	8.8	0.3523	II	$\exp(1.3c)/5.7c$
23	4.8	−2.4	2	II	$\exp(3.6c)/2.4c$
32	−2.4	−2.4	−1	I	$1/2.4c$

Using (9), $\phi_{ij} = 1/NI_{ij}$ we see that ϕ_{21}, ϕ_{31}, and ϕ_{32} are exponentially small, so marking the small terms with *'s, we have the same pattern as in the previous example.

$$D\pi_1 = \phi^*_{31}\phi_{21} + \phi_{32}\phi_{21} + \phi^*_{23}\phi^*_{31} \approx 2.4(3.2)c^2$$
$$D\pi_2 = \phi^*_{12}\phi_{32} + \phi_{13}\phi_{32} + \phi^*_{31}\phi^*_{12} \approx 5.7(2.4)c^2$$
$$D\pi_3 = \phi^*_{23}\phi_{13} + \phi_{21}\phi_{13} + \phi^*_{12}\phi^*_{23} \approx 3.2(5.7)c^2$$

so for large c we have $3 > 2 > 1$. Comparing this with the small c ranking of $2 > 1 > 3$ we can see that there must be two ranking changes to bring strategy 3 from last to first.

12 Discussion

sec:disc

In this paper we have developed methods for computing strategy rankings when mutation rates are small, the strength of selection is c/N, and the population size $N \to \infty$. For any c the rankings can be computed by numerically evaluating an integral. We have simple explicit results when c is small or c is large. We have treated five examples to illustrate the method, but the conclusions in those examples have led us to question the accuracy of rankings obtained by considering extremely small mutation rates.

In Example 2, the mixed strategy of the 1,2 subgame is attracting, while $3 \gg 1$ and $2 \gg 3$. This situation can be drawn as:

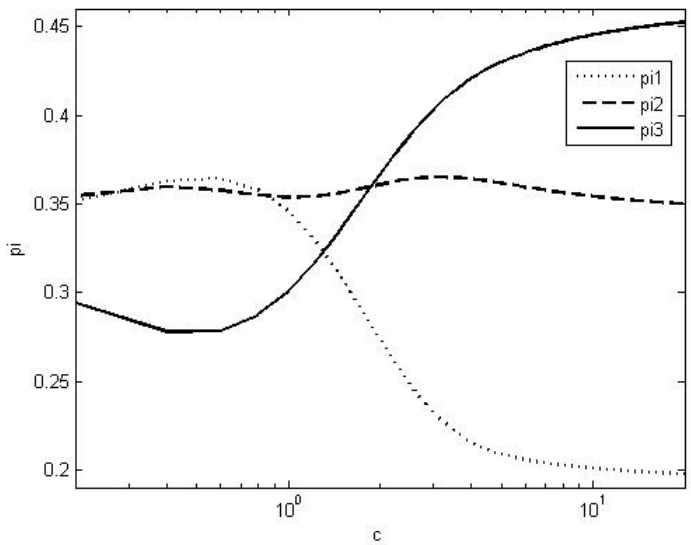
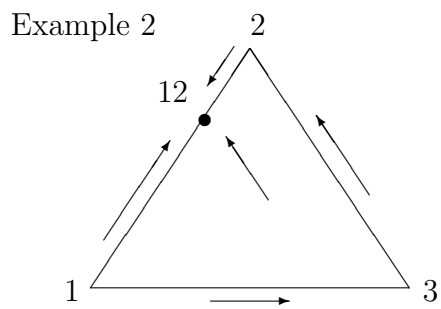


Figure 6: Plot of rankings versus $\log(c)$ in Example 5. fig:figure



The calculation for Example 2 shows that it is very unlikely for 1 to invade and replace 2. However it is not difficult for 1 to invade and bring the system to the mixed strategy equilibrium for the 1,2 subgame in which there are $M = N/3$ individuals playing strategy 1. To show this we use 12 to denote the equilibrium and combine (5) and (7) to conclude

$$\begin{aligned}\frac{1}{N}h(M) &\to \int_0^{1/3} \exp(-c[a_{12}x - (a_{12} + a_{21}x^2/2])\,dx \\ &\to \int_0^{1/3} \exp(-c[2x - 3x^2])\,dx\end{aligned}$$

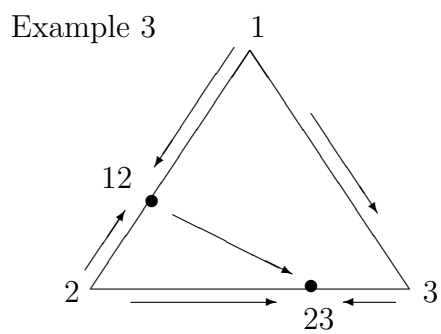
The derivative of $-(2x - 3x^2)$ is $-2 + 6x$ which is 0 at $x = 1/3$, < 0 for $x < 1/3$ and > 0 when $x > 1/3$, so if c is large

$$I_{2,12} = \int_0^{1/3} \exp(-c[2x - 3x^2])\,dx \approx \int_0^{\epsilon} \exp(-2cx)\,dx = \frac{1}{2c}$$

and using (6) we have

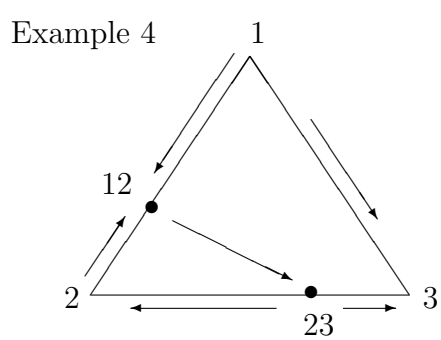
$$\phi_{2,12} \approx 2c/N$$

If the mutation rate per individual is ν/N then mutations will occur at rate ν in the population and the time until a successful mutation takes us to 12 has mean $\nu N/(2c)$. By computing the Green's function of the birth and death chain (results not shown) one can show that the process will stay near the mixed strategy equilibrium for time $O(N^2)$, so in the long run most of the time will be spent near 12, making it the solution in the weak mutation limit, a conclusion that does not change as the strength of election is changed. Of course if the mutation rate $\mu = o(N^{-2})$ then the pure strategies will last longer than the mixed one.



Example 3 has similar issues to Example 2 but has a new feature. The process stays near 12 for a long time but during that period the 3's may invade and take the process to the 23 mixed strategy equilibrium, while it is very unlikely for mutations to take the process back to 13. Computing invasion probabilities for mixed strategy fixed points is not easy. Indeed it was the desire to avoid using the theory developed by Freidlin and Wentzell [3] that motivated Fudenberg and Imhof to investigate the small mutation limit. However, it seems that this problem that needs to be addressed to get sensible results.

Example 4 is perhaps the most difficult of the examples considered here. Both 12 and 3 are locally attracting, so it is difficult to determine which of these will be the true equilibrium.



Finally in the rock-paper-scissors game in Example 1, the trip around the outside of the triangle which occurs in the small mutation limit may be unstable leading to the system spiraling into a fixed point.

In summary, the answers obtained for the small mutation limit are based on a consideration of the three 2×2 subgames. They do not consider the possibility of three strategy coexistence that can occur when the per individual mutation rate $\mu = O(1/N)$. Our calculations show that the small mutation limit in some cases requires $\mu = o(N^{-2})$, which may not be reasonable for some applications.

When this paper was completed when did not realize that it was "well-known" that stable mixed strategy equilibria were problematic for the small mutation limit. Antal and Scheuring [1] discussed this for 2×2 games. Wu, Gokhale, Wang, and Traulsen [12] went further and quantified how small mutation rates should be. While for a coexistence game, where the best reply to any strategy is the opposite strategy, it is necessary that the mutation rate is less than $N^{-1/2} \exp(-N)$ to ensure that the approximation is good, for all other games, it is sufficient if themutation rate is smaller than $(N \ln N)^{-1}$. Their results assume the strength of selection is fixed while $N \to \infty$. In our weak selection limit $o(N^{-2}$ is sufficent for all casses.

Acknowledgements

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