Stochastic Evolution as a Generalized Moran Process

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Abstract:

This paper proposes and analyzes a model of stochastic evolution in finite populations. The expected motion in our model resembles the standard replicator dynamic when the population is large, but is qualitatively different when the population size is small, due to the difference between maximizing payoff and maximizing relative payoff. Moreover, even in large populations the asymptotic behavior of our system differs from that of the best-response and replicator dynamics due to its stochastic component.

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1.   Introduction

This paper proposes and analyzes a model of stochastic evolution in finite populations.   Our model is a generalization of the Moran process of evolutionary biology (Moran [1962],   Ewens [2004]) to frequency-dependent fitness. In this process, one individual per period "dies" and is replaced by a newcomer. The newcomer's strategy is a random variable whose distribution is given by an "updating function" that depends only on the current state, that is, the numbers of agents using each choice.

The updating function we study has two parts, the "base rate" updating rule and a lower-frequency probability of "mutation." In the base-rate or "unperturbed" process, each agent has a number of "offspring" that is equal to its payoff in the game, and the new agent is chosen at random from the pool of all the offspring. [1] This process can also be interpreted as a model of imitation: Each period, one randomly chosen individual re-evaluates its choice, with the probability of choosing a given strategy equal to the total payoff of players using that strategy divided by the total payoff in the population, so that the choice depends on both the payoff of each strategy and on the strategy's popularity.[2]

In the spirit of the literature on large deviations, we relate the long-run behavior of the process with mutations to that of the simpler process where mutations are absent. In this unperturbed process, every monomorphic configuration is a steady state. The mutations lead to a fluctuation between these configurations; our analysis determines the limit of this distribution as the frequency of mutation goes to 0.

Most of this paper analyzes the case of symmetric 2x2 games. The analysis differs from past applications of large deviations theory to such games because the limit distribution is not a point mass. Instead, the relative probabilities of the various states depend on the transition probabilities of the base-rate process. After obtaining the

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[1] In the classic Moran process, the fitness of each strategy is independent of the state of the population. In the evolutionary interpretation of the model, the assumption of an exogenous finite population size can be viewed as an approximation to a model where environmental forces keep the population from becoming infinite.

formula for the limit distribution in terms of the parameters of the payoff matrix, we then classify games according to which strategy is favored. In some cases one strategy is favored for any population size, and the probability assigned to the favored strategy converges to 1 as $N \rightarrow \infty$. In other cases, the favored strategy depends on the population size. This is true in particular for the case where B is the dominant strategy, but the payoff of playing A against B exceeds the payoff of playing B against A. Here there is a "spite" effect when the population is sufficiently small: Even though strategy A is dominated, it can be long-run outcome of the evolutionary process, since for example strategy A has higher payoff than strategy B when each strategy is played by exactly one agent. However, as the population grows, the difference between absolute and relative performance vanishes, and the evolutionary process selects the dominant strategy B.

The selected equilibrium can also depend on population size in some games with two pure-strategy equilibria. Moreover, in such games the risk-dominant equilibrium need not be selected, even in the limit of large populations., in contrast to the work of Kandori, Mailath, and Rob [1993] (KMR) and Young [1993] on 2x2 games. This is because those papers analyze deterministic no-mutation processes, so that the equilibrium selected is determined by comparison of the "radii" (Ellison [2000]) of the absorbing states, while we analyze a stochastic no-mutation process, where a single mutation can lead to a transition from one absorbing state of the no-mutation process to the other. Thus, the equilibrium that is selected depends on the "expected speed of the flow" at every point in the state space, and two coordination games with the same mixed-strategy equilibrium (and hence the same basins for the best-response and replicator dynamic[3]) can have systematically different speeds at other states.[4] However, the risk-dominant equilibrium is selected when payoffs from the game have only a weak effect on the overall fitness of the strategy.

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[2] Giving weight to popularity as well as current payoffs is a rule of thumb that allows current choices to in effect depend on past states of the system. Ellison and Fudenberg [1993, 1995] show that such rules can be socially beneficial.

[3] By "replicator dynamic " here we mean the standard version with linear fitness functions, which is due to Taylor and Jonker [1978]; see Fudenberg and Levine [1998], and Hofbauer and Sigmund [1998], [2003] for surveys of related results

[4] See Fudenberg and Harris [1992] for a discussion of why one should expect stochastic stability to depend on the "speed of the flow" as well as on the expected direction of motion.

To understand the behavior of our model for large *N,* it is helpful to note that its mean field (that is, expected motion) converges to that of the standard replicator dynamic as the population becomes infinite.[5] Thus, the results of Benaim and Weibull [2003a,b] show that for large N the state of the process will, with high probability, remain close to the path of the deterministic replicator dynamic for some large time T.[6] However, just as in that paper, even for large N the asymptotics of the stochastic system depend on the details of the stochastic structure, and can differ from those of the deterministic replicator dynamic. Moreover, our finding that the risk-dominant equilibrium need not be selected shows that the asymptotic behavior of our system can differ from that of the stochastic replicator dynamic studied by Fudenberg and Harris (FH) [1992]. FH assumed that the payoffs to each strategy profile were subject to a random aggregate shock that was modeled as a diffusion, and derived a diffusion process for the population shares using each strategy; this process converges to the risk-dominant equilibrium as the variance of the aggregate shock goes to 0. In this context, it is interesting to note that our process does pick out the risk-dominant equilibrium in the case of weak selection; this is the case where the asymptotics of our system can be approximated by a diffusion.

In addition to our classification of the limit distribution in all 2x2 games, we analyze the limit distribution in 3x3 coordination games with large populations. For generic payoffs the limit distribution converges to a point mass as the population goes to infinity, but even when a ½ -dominant equilibrium exists it need not be selected, for much the same reason that the risk-dominant equilibrium need not be selected in 2x2 games.

The possibility of a "spite effect" in finite populations was pointed out by Hamilton [1970], and led Schaffer [1989] to propose an alternative definition of evolutionary stability for finite populations. Rhode and Stegeman [1994] analyze the effect of spite in the "Darwinian" model of KMR, which supposes that the unperturbed dynamic is deterministic; they show that even allowing for spite the risk-dominant equilibrium is selected in large populations. Our process yields a different conclusion.

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[5] Note that in small populations the mean field in our model can be very different from that of the replicator due to the difference between maximizing absolute and relative performance.

[6] One can instead obtain a diffusion approximation if the payoffs in each interaction are scaled with the population size in the appropriate way, see e.g. Binmore et al [1995].

Fogel et al [1998] and Ficci et al [2000] report some simulations of the "frequency-dependent roulette wheel" selection dynamic, which is equivalent to the generalized Moran process we analyze.[7] This paper, and its companion Taylor et al [2004], present analytic results for the case of fixed finite populations. Taylor et al look at the process without mutations, and compare the probability that the state where a single agent plays *A* (with the others playing *B*) is absorbed at the state "all *A*" to the corresponding fixation probability in the neutral case where A gives the same payoff as B at each state.[8] This paper differs in its assumption of recurrent mutations, and also in the nature of its conclusion: We provide a simple sufficient condition on the payoff matrix for the limit distribution to assign probability greater than ½ to all agents playing A, and for it to assign probability 1 to this state when the population is large.

2.   The Model

To begin, and in most of the paper, we consider a population of N agents playing a 2x2 symmetric game. This game has payoff matrix

$$
\begin{array}{cc}
 & A \qquad B \\
\begin{array}{c} A \\ B \end{array} & \left(\begin{array}{cc} a,a & b,c \\ c,b & d,d \end{array} \right),
\end{array}
$$

where *a, b, c,* and *d* are all strictly positive. The state of the system, denoted *s,* is the number of individuals using strategy *A*. Agents are matched with each opponent from the population, but the importance of each interaction is inversely proportional to the number of interactions, so that when there are *s* agents playing *A,* the fitness of individuals using strategy *A* is given by $f_s = \dfrac{a(s-1)+b(N-s)}{N-1}$ and the fitness of

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[7] Fogel et al emphasize that the finite population results can be very different than the predictions of the replicator equation, while Ficci et al argue that the two models make fairly similar predictions in the hawk-dove game.

[8] This neutral selection probability is $1/N$. Nowak et al [2004] apply these results on the no-mutation process to the comparison of the strategies "Always Cooperate" and "Tit for Tat" in the finitely repeated prisoner's dilemma.

individuals using strategy B is given by $g_s = \dfrac{cs + d(N - s - 1)}{N - 1}$.[9] Note that at a fixed state

the two types of agent face a slightly different distribution of opponents' play. This fact is what underlies the difference between maximizing relative payoff and maximizing absolute payoff.

The distribution of strategies in the population evolves as follows. Each period, each agent "reproduces" at a rate proportional to its fitness, so that the number of A-offspring is sf_s and the number of B-offspring is $(N - s)g_s$. One offspring is chosen at random[10] to enter the population, so that the probability of adding an A offspring is

$\dfrac{sf_s}{sf_s + (N - s)g_s}$. However, there is a probability μ_{AB} that an A-offspring is a "mutant"

that plays B instead of A, and a probability $\mu_{BA} = k\mu_{AB}$ that a B-offspring plays A instead of B. Finally, after reproduction, one randomly chosen agent is removed from the population, so that the aggregate population size is constant; each old agent has probability 1/N of being removed. As we remarked earlier, this process can be viewed as a model of imitation, as opposed to evolution: Each period one agent at random is selected to update, and the choice of a new strategy is influenced both by the prevailing payoffs and the prevailing popularity of the choices. [11] Note also that this is a "birth-death" process: the states are integers, and in each period the state can move by at most one step. [12]

To define the process formally, let $P_{s,r}$ denote the probability of a transition from state s to state r. Then

$$P_{s,r} = 0 \text{ if } |s - r| > 1, \quad P_{0,1} = \mu_{BA} = 1 - P_{0,0}, \quad P_{N,N-1} = \mu_{AB} = 1 - P_{N,N},$$

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[9] Robson and Vega-Redondo [1996] analyze a model where agents are randomly paired, and evolution is governed by the realized average payoffs of the strategies, which depend on the outcome of the matching process. In their model, the limit as the number of rounds goes to infinity of the limit distributions (i.e. of the limit of the ergodic distributions as the mutation rate vanishes) can be different that the limit distribution with an infinite number of rounds, but as we explain later that is not the case here.

[10] That is, each offspring has equal probability, namely $\left(sf_s + (N - s)g_s\right)^{-1}$.

[11] Giving weight to popularity as well as current payoffs is a rule of thumb that allows current choices to in effect depend on past states of the system. Ellison and Fudenberg [1993, 1995] show that such rules can be socially beneficial when there are stochastic shocks to the payoff functions.

[12] Kirman [1993] looks at a birth-death model of imitation that is not explicitly linked to game payoffs, and characterizes the limit of the ergodic distribution when the mutation rate goes to 0 at rate 1/N.

and for s = 1 to *N*-1 we have

$$P_{s,s+1} = \frac{sf_s(1-\mu_{AB})+(N-s)g_s\mu_{BA}}{sf_s+(N-s)g_s}\frac{N-s}{N},$$

$$P_{s,s-1} = \frac{sf_s\mu_{AB}+(N-s)g_s(1-\mu_{BA})}{sf_s+(N-s)g_s}\frac{s}{N}, \text{ and}$$

$$P_{s,s} = 1 - P_{s,s+1} - P_{s,s-1}.$$

Because of the presence of mutations, this process is ergodic, with a unique invariant distribution that we denote $x(\mu_{AB},\mu_{BA},N)$.

Let $\hat{P}$ be the version of the process where the mutation rates are identically zero. Thus, under $\hat{P}$ the transition probabilities are

$$\hat{P}_{0,0} = 1$$

$$\hat{P}_{s,s+1} = \frac{sf_s}{sf_s+(N-s)g_s}\frac{N-s}{N}, \quad \hat{P}_{s,s-1} = \frac{(N-s)g_s}{sf_s+(N-s)g_s}\frac{s}{N}, \text{ and}$$

$$\hat{P}_{s,s} = 1 - \hat{P}_{s,s+1} - \hat{P}_{s,s-1} \qquad \text{for } s = 1 \text{ to N-1,}$$

and $\hat{P}_{N,N} = 1$.

Note that $\dfrac{\hat{P}_{s,s-1}}{\hat{P}_{s,s+1}} = \left(\dfrac{(N-s)g_s}{sf_s+(N-s)g_s}\dfrac{s}{N}\right)\bigg/\left(\dfrac{sf_s}{sf_s+(N-s)g_s}\dfrac{(N-s)}{N}\right) = \dfrac{g_s}{f_s}$: the ratio of the

transition probabilities equals the ratio of the fitness levels. [13]

In this process, states 0 and N are absorbing, and the others are transient. Thus, from the work of Freidlin and Wentzell [1984], we expect that the invariant distribution for small μ will be concentrated on these two endpoints. Intuitively, after each

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[13] Here is another model that gives rise to the same long-run outcome: Each period, a single agent at random is chosen from the population, and matched (without replacement) with a single second agent. The first agent "reproduces" with probability equal to its realized payoff divided by a scale factor z that is larger than $\max\{a,b,c,d\}$. If the agent reproduces, it replaces a randomly chosen member of the entire population. Thus for example the probability of an increase in the number of A players is the probability an A is chosen times the expected payoff of an A times the probability a B is replaced times z, so that

$P'_{s,s+1} = (s/N)[(s-1)a+(N-s)b]((N-s)/N)/z$, and $\dfrac{P'_{s,s+1}}{P'_{s,s-1}} = \dfrac{f_s}{g_s} = \dfrac{\hat{P}_{s,s+1}}{\hat{P}_{s,s-1}}$, so the new process differs from

the original one only in its speed.

mutation, the process will reach an absorbing state of the no-mutation process and remain there for a long time before the next mutation occurs. We will verify this intuition, and refine it by computing the relative probabilities of states 0 and N.

We now want to hold fixed N and $k = \mu_{BA} / \mu_{AB}$, where we assume that $0 < k < \infty$, and vary the scale of the mutations. Let $x^*(k, N) \equiv \lim_{\mu_{AB} \to 0} x(k, \mu_{AB}, k\mu_{AB})$. We call $x^*(k, N)$ the "limit distribution;" it describes the long-run distribution of strategies when mutations are extremely rare.

The literature on large deviations shows that the limit distribution is concentrated on the attractors of the limit process, which in our case are the states N (all A) and 0 (all B) [14] Henceforward, to simplify notation we will regard $x^*(k, N) = \left(x_A^*(k, N), x_B^*(k, N) \right)$ as a probability vector on these two states, instead of on the entire state space. The literature also suggests that the transition probabilities in the mutationless process $\hat{P}$ play a key role in determining the limit distribution. In our case, the relevant probabilities are those for transitions from state 1 (where almost everyone plays B) to state N (where everyone plays A), which we denote ρ_{BA} and the probability of absorption at 0, starting at N-1, denoted by $\rho_{A,B}$.

Lemma 1: The weights $\left(x_A^*(k, N), x_B^*(k, N) \right)$ that the limit distribution assigns to states "all A" and "all B" are $\dfrac{k\rho_{BA}}{k\rho_{BA} + \rho_{AB}}$ and $\dfrac{\rho_{AB}}{k\rho_{BA} + \rho_{AB}}$ respectively.

Proof: This follows from the theorem of Fudenberg and Imhof [2004]. [15] For a heuristic derivation, consider the embedded Markov chain on the two states 0 and N, where the transition out of each state occurs with a single mutation. That is, we ignore all periods where the state has value other than 0 or N, and set the probability of a transition from state 0 to state N to $\mu_{BA}\rho_{BA}$, and the probability of a transition out of state N to $\mu_{AB}\rho_{AB}$. The key assumption is that this embedded chain has a unique invariant

[14] See for example Kifer [1990] Theorem 3.1.
[15] See the earlier version of this paper (Fudenberg et al 2004) for a direct proof.

distribution, which it will if both these terms are positive; the displayed formula is simply the invariant distribution of this chain. [16]

This formula shows that the long-run distribution is a continuous function of the absorption probabilities of the no-mutation process so long as these probabilities are bounded away from 0.

Lemma 2: $\qquad \phi_{BA} = \dfrac{1}{1 + \sum_{r=1}^{N-1} \prod_{s=1}^{r} \dfrac{g_s}{f_s}}$, and

$$\phi_{AB} = \frac{\prod_{s=1}^{N-1} \dfrac{g_s}{f_s}}{1 + \sum_{r=1}^{N-1} \prod_{s=1}^{r} \dfrac{g_s}{f_s}}.$$

Proof: This is an easy consequence of a result given in Karlin and Taylor, p. 113, exercise 4. The general formula depends on the ratios of the one-step transition probabilities; the simple functional form in the lemma is due to the fact that $\dfrac{\hat{P}_{s,s-1}}{\hat{P}_{s,s+1}} = \dfrac{g_s}{f_s}$.

Remark on Random Matching: If players are randomly matched ν times instead of playing each other agent exactly once, the number of A and B offspring will be a stochastic function of the state, and the transition and absorption probabilities will not have exactly the form of lemma 2. However, the law of large numbers shows that the probabilities will converge to the same limit, so the limit distribution with payoffs exactly equal to their expected values (which corresponds to $\nu = \infty$) is equal to the limit of the ergodic distributions $x^*(k, N, \nu)$ as $\nu \to \infty$.[17] The work of Boylan [1992] suggests that a similar argument holds in the limit $N \to \infty$: That is, if agents are randomly paired to play the game, and each agent only plays once before the population is updated, the limit distribution should close to that of our model when N is large.

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[16] For the embedded chain to have a unique invariant distribution, the no-mutation process can have at most one absorbing state whose radius (in the sense of Ellison [2000]) exceeds 1. Noldeke and Samuelson [1993] consider a process on extensive form games where many absorbing states have radius 1.
[17] In Robson and Vega-Redondo [1996], the basin of the Pareto-efficient equilibrium has radius 2 (in the sense of Ellison [2000]) when ν is finite, but basin proportional to population size when ν is infinite, so the selected equilibrium depends on the order of limits.

However, since changing N changes the state space of the stochastic process, the argument is more complicated, and we have not verified that it holds.

Lemmas 1 and 2 yield the following corollary, which provides the basis for our main conclusions. Let $\gamma = \prod_{s=1}^{N-1} \frac{f_s}{g_s}$.

Lemma 3:   i) $x_A^*(k,N) == \dfrac{k \prod_{s=1}^{N-1} f_s}{k \prod_{s=1}^{N-1} f_s + \prod_{s=1}^{N-1} g_s} = \dfrac{k\gamma}{k\gamma+1}$.

ii) $x_A^*(k,N) > 1/2$ exactly when $\gamma > 1/k$.

iii) $x_A^*(k,N)$ converges to 1 or 0 as γ converges to ∞ or 0 respectively.

In previous work on limit distributions in 2x2 games, such as Kandori, Mailath, and Rob [1993], Young [1993], and Robson and Vega-Redondo [1996], the ratio of the mutation probabilities (here, the parameter k) has no effect on the limit distribution so long as it is bounded away from 0 and infinity.[18] This dependence on the ratio of the two sorts of mutations is a consequence of the fact that for fixed N the limit distribution assigns positive probability to more than one point, which in turn is related to the fact that both attractors have radius 1.

3.   Implications for Games

We now use Lemma 3 to study how the limit distribution depends on the size of the population and on the parameters of the payoff matrix. To this end, we substitute the values of the fitness functions at each state into the equation for γ:

$$\gamma = \frac{((N-1)b)((N-2)b+a)....(b+(N-2)a)}{(c+(N-2)d)(2c+(N-3)d)...((N-2)c+d)((N-1)c)}$$

$$= \frac{(b+(N-2)a)...((N-2)b+a)((N-1)b)}{(c+(N-2)d)...((N-2)c+d)((N-1)c)}. \tag{1}$$

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[18] Bergin and Lipman [1996] study what can happen in the Kandori et al model when k is state-dependent and tends to 0 at some states as the overall mutation probability goes to 0.

As a preliminary step, note that when $N = 2$, $\gamma = b/c$, so that strategy A is favored when $b > c$ and $k = 1$. Intuitively, every time there is a mutation, the system moves to the state $s = 1$ with one A and one B, and at this state, the relative fitness of the two strategies is determined by their payoffs when playing each other. Our results will follow from a more detailed analysis of the ratio in (1). Note also that multiplying all of the payoffs by a constant has no effect on γ, and so has no effect on the limit of the ergodic distributions. However, γ may change when a constant is added to all of the fitness functions. This observation is related to our results in the next section on weak selection.

To cut down on cases, we assume now that $b > c$. This can be done by re-labeling except for the knife-edge case where $b = c$. The next theorem further specializes to the case where $k = 1$, so that both sorts of mutations are equally likely; we return to the case of general k when considering the large population limit in theorem 2.

<u>Theorem 1:</u>

    (a)   If $b > c, a > d$, then $x_A^*(1, N) > 1/2$ for all N.

    (b)   If $b > c, a < d$, then whether $x_A^*(1, N) > 1/2$ depends on the population

                size. A sufficient condition for $x_A^*(1, N) > 1/2$ is $b - c > (N - 2)(d - a)$.

Proof: In case (a), the first term in the product in the numerator of the final ratio in (1) exceeds the corresponding term in the denominator, as does the second, etc, so that $\gamma > 1$, and lemma 3 implies that $x_N^*(1, N) > 1/2$.

In case (b), if $b + (N - 2)a > c + (N - 2)d$, the pairwise comparison of terms again shows that $\gamma > 1$, and $b + (N - 2)a > c + (N - 2)d$ is equivalent to $b - c > (N - 2)(d - a)$.   ■

Theorem 1 gives results for any *N*, but here both strategies have positive weights, and the ratio of the weights depends on the ratio of the mutation probabilities. However, the effects of the payoff matrix overwhelm the effect of the ratio of the mutation

probabilities when the population is sufficiently large, which is one reason for interest in the case of population sizes tending to infinity. A second reason for studying this case is to see how well it is captured by the replicator dynamic, which corresponds to the behavior of the system in a continuum population. (That is, the replicator is the mean field of this system.)

Theorem 2:   For any *k:*

a)   If $b > c, a > d$, then, $\lim_{N \to \infty} x_A^*(k, N) = 1$.

(b.1)   If $b > d > a > c$, $\lim_{N \to \infty} x_A^*(k, N) = 1$.

(b.2)   If $d > b > c > a$, $\lim_{N \to \infty} x_A^*(k, N) = 0$.

(b.3)   If $d > b > a > c$ or $d > a > b > c$, there are two pure-strategy Nash equilibria, and $\lim_{N \to \infty} x_A^*(k, N)$ is either 1 or 0

as $\int_0^1 \ln(b + (a - b)x)dx$ is greater or less than

$\int_0^1 \ln(d + (c - d)x)dx$.

The risk-dominant equilibrium need not be selected.

Proof: In case a), the ratio of each pair of terms in γ is bounded away from 1, so $\gamma \to \infty$ as $N \to \infty$. Thus lemma 3 implies that $\lim_{N \to \infty} x_N^*(k, N) = 1$. In subcases (b.1) and (b.2), we examine the expression in the first line of (1): in subcase (b.1), every term in the numerator exceeds the corresponding term in the denominator, and in (b.2) the reverse is true provided that $N - 2 > (b - c)/(d - b)$ and $N - 2 > (b - c)/(c - a)$. The argument for large *N* in subcase (b.3) involves approximating γ by the ratio of two integrals, using $\prod_{s=0}^{N-1}\left[a\frac{s}{N - 1} + b(1 - \frac{s}{N - 1})\right] = \exp\left(N\int_0^1 \ln(a + (b - a)x)dx\right) + O(1)$; the details are in the appendix.   ∎

We will say that a strategy is "favored" by the evolutionary process if its probability under the limit distribution is greater than ½ when $k = 1$; we will say that the

strategy is "selected" if its probability under the limit distribution goes to 1 as N goes to infinity. This language will make it easier to discuss the conclusions of the theorems.

The class of games in case (a) is composed of games where A is strictly dominant ($a > b > c > d$ $a > b > d > c$, $b > a > d > c$, and $b > a > c > d$), coordination games where A,A is both Pareto-dominant equilibrium and risk-dominant [19] ($a > d > b > c$), and "hawk-dove" games with two asymmetric equilibrium and a equilibrium in mixed strategies ($b > c > a > d$). When A is strictly dominant, it is selected by the deterministic replicator dynamic from any initial position, and it is not surprising that the same thing happens here as N goes to infinity. It is similarly unsurprising that A is selected when it is both risk and Pareto-dominant: Although both of the Nash equilibria are asymptotically stable in the deterministic replicator dynamic, past work on stochastic evolutionary models has always selected any strategy that is both risk and Pareto dominant.

In case (b), $b > c$, so we expect that A will be favored for small N. In subcase (b.1), A is the dominant strategy, so this tendency is reinforced for large N. In subcase (b.2), B is dominant, and is selected for large N, but A is favored for small N, as in example 1 below; this is the "spite" effect that we mention in the abstract.

Subcase (b.3), where (A,A) and (B,B) are both pure-strategy equilibria, is more complex. Past work has concluded that the long-run distribution is concentrated on the risk-dominant equilibrium.[20] However, that need not be the case here. This is easiest to see by considering a game where $d > b > a > c$, and $a + b = c + d$ so that neither strategy is risk dominant. Then the two integrals are the expectations of the logarithm of two random variables with the same mean. Because the log is a concave function, the expected value of the log is reduced by a mean-preserving spread, and so (A,A) is selected because $b - a < d - c$. Intuitively, the condition $a + b = c + d$ implies that the two strategies are equally fit at the point $s = N/2$, but the support of the long-run distribution depends on the transition probabilities at every state, and these are not determined by the value of the fitness functions at the midpoint.

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[19] In a 2x2 game, a strategy is risk dominant if it is the unique best response to the distribution $(.5A,.5B)$. In Kandori et al [1993] and Young [1993], the risk dominant equilibrium is selected as the mutation rate goes to 0. That is, the limit of the ergodic distributions as the mutation rate goes to 0 is a point mass on the risk-dominant equilibrium.

Both case (a) and case (b) include subcases that correspond to "hawk-dove games," that is symmetric games with two asymmetric pure-strategy equilibria. Since we are working in a one-population model, the asymmetric equilibria in the hawk-dove case cannot arise, but the conclusion that the process spends almost all of its time in homomorphous states may seem odd. This conclusion is a consequence of our focus on the limits of the ergodic distribution for the case of vanishingly small mutation rates; when the population size is large compared to θ the distribution is concentrated near the mixed equilibrium.[21]

We summarize the above discussion of our results for large populations by regrouping cases according to more traditional game-theoretic criteria.

Corollary: If the game has a strictly dominant strategy, the probability assigned this strategy by the limit distribution converges to 1 as N goes to infinity. If the game has two strict Nash equilibria, then except for knife-edge cases there is an equilibrium to which the limit distribution assigns probability converging to 1 as N goes to infinity, but the risk-dominant equilibrium need not be selected.

4.   3x3 Coordination Games

Now consider a 3x3 symmetric game with pure strategies 1,2,3, and strictly positive payoff matrix $\{a_{ij}\}_{i,j=1}^{3}$, where a_{ij} is the payoff for strategy *i* playing strategy *j*. As before, there is a fixed population of *N* agents; the state *s* of the system is the number of agents using each strategy. We denote the fitness of strategies 1, 2, and 3 by f_s, g_s, and h_s respectively, where for example $f_s = \dfrac{(s_1 - 1)a_{11} + s_2 a_{12} + s_3 a_{13}}{N - 1}$. The no-mutation process is again constructed by assuming that each agent playing strategy *i* has a number

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[20] Strategy *A* is risk dominant if $a + b > c + d$, and *B* is risk dominant if the reverse inequality holds. When *A* is risk-dominant, it is the best response to the mixed strategy (½ A, ½ B).
[21] The work of Benaim and Weibull [2003a,b] suggests that the limit as $N \to \infty$ for a fixed mutation rate should be one of the attractors of the mean field of the process. In the case of coordination games, these attractors are the pure-strategy equilibria, which are also the support of the limit distribution. Moreover, we conjecture that in coordination games, the equilibrium selected by first sending the mutation rate to 0 and then sending the population size to infinity, as in Theorem 2, is the same as the one selected with the other order of limits. This conjecture is explored in a more general setting in work in progress by Fudenberg and Hojman [2004].

of offspring equal to its payoff, with one offspring chosen at random to replace a random member of the current population, so that e.g. the probability that a 1-user replaces a 2-user is $\dfrac{s_1 f_s}{s_1 f_s + s_2 g_s + s_3 h_s} \dfrac{s_2}{N}$, and the ratio of this probability to that of a move in the other direction is $\dfrac{f_s}{g_s}$, just as it was in the two-strategy case. Let $\rho_{ji}(N)$ be the probability that under the no-mutation process is absorbed at the homogeneous state where all agents play i, starting from the state where only one agent plays i and all the rest play j. Since the no-mutation process never introduces an extinct strategy, $\rho_{ji}(N)$ is the same as if the game only had these two strategies.

We add mutations to the system by supposing that there is common probability μ that the offspring of an i-strategist is a j-strategist. We let $x^*(N)$ denote the limit of the ergodic distributions as $\mu \to 0$. As before we represent this as a probability distribution over the homogeneous states instead of as a distribution over the entire state space, so that $x_i^*(N)$ is the probability that the limit distribution gives to the state "all i.".

Lemma 4: The limit distribution as μ goes to 0 is

$x^*(N) = (x_1^*(N), x_2^*(N), x_3^*(N))$, where

$$x_i^*(N) = \frac{\left(\rho_{ji}(N)\rho_{ki}(N) + \rho_{ji}(N)\rho_{kj}(N) + \rho_{ki}(N)\rho_{jk}(N)\right)_{i \neq j \neq k}}{\sum_{r=1}^{3} \rho_{jr}(N)\rho_{kr}(N) + \rho_{jr}(N)\rho_{kj}(N) + \rho_{kr}(N)\rho_{jk}(N)_{r \neq j \neq k}} .$$

Proof: This is example 2 of Fudenberg and Imhof [2004]. Note that the formula given is that for the invariant distribution of a Markov chain on the three states i, j, k, whose off-diagonal transition probabilities are given by the ρ's. ∎

We now specialize to the coordination-game case, where each of the pure strategies corresponds to a symmetric Nash equilibrium, so that $a_{ii} > a_{ji}$ for all i and $j \neq i$. From the 2x2 case, know that the ρ_{ij} will all be positive, so lemma 4 implies that the limit distribution will give positive probability to each strategy in a population of fixed size. Our goal is to determine the behavior of the limit distribution as the

population size N goes to infinity. To do so, we will characterize the limit on N of the $\rho_{ij}(N)$ in terms of integrals of logarithms of the relative fitness of strategies i and j, using an argument that is similar in spirit but more complex than that in the proof of Theorem 2, case b.3. To this end let $z_{ji}^* = \dfrac{a_{jj} - a_{ij}}{a_{jj} - a_{ij} + a_{ii} - a_{ji}} = 1 - z_{ij}^*$; this is the weight given to strategy i in the mixed equilibrium in the 2x2 subgame corresponding to strategies i and j, and is strictly between 0 and 1 because we have specialized to coordination games. Define $\phi_{ji}(z) = \ln\left[\dfrac{a_{ji}z + a_{jj}(1-z)}{a_{ii}z + a_{ij}(1-z)}\right]$; this is the logarithm of the ratio of the expected payoffs of j and i in an infinite population where fraction z plays i and all the rest play j. Finally define $\beta_{ji} = \int_0^{z_{ji}^*} \phi_{ji}(z)dz$; note that this is strictly positive.

Lemma 5: There are constants $0 < m < M < \infty$ such that for all $N \geq 2$, and all pairs of distinct strategies i,j, $m \leq N^{1/2} \exp(N\beta_{ji}) \rho_{ji}(N) \leq M$.

The proof of this is in the appendix. Here is a sketch: We first argue that $1/\rho_{ji}(N)$ is bounded above and below by terms proportional to $N \int_0^1 \exp\left((N-1)\psi(z)\right)dz$, where $\psi(z) = \int_0^z \phi(t)dt$. We then use the "Laplace method" (de Bruijn 1958]) to approximate $\int_0^1 \exp\left((N-1)\psi(z)\right)dz$. In essence, this method is to first approximate $\int_0^1 \exp\left((N-1)\psi(z)\right)dz$ by $\int_{z^*-\varepsilon}^{z^*+\varepsilon} \exp\left((N-1)\psi(z)\right)dz$, where $z^* = \arg\max(\psi(z))$, and the approximate $\int_{z^*-\varepsilon}^{z^*+\varepsilon} \exp\left((N-1)\psi(z)\right)dz$ by $\int_{z^*-\varepsilon}^{z^*+\varepsilon} \exp\left((N-1)\tilde{\psi}(z)\right)dz$, where $\tilde{\psi}$ is the second-order Taylor approximation to ψ.

Theorem 3: Let $\gamma_i = \min\{\beta_{ji} + \beta_{ki}, \min_j(\beta_{ji} + \beta_{kj})\}_{i \neq j \neq k}$, and let $\gamma^* = \min_i \gamma_i$.

Then for every j with $\gamma_j > \gamma^*$, $\lim_{N \to \infty} x_j^*(N) = 0$. In particular, if $\gamma_i < \min(\gamma_j)_{j \neq i}$

then $\lim_{N \to \infty} x_i^*(N) = 1$.

Proof: From lemma 4, $\dfrac{x_i^*(N)}{x_j^*(N)} = \dfrac{\rho_{ji}(N)\rho_{ki}(N) + \rho_{ji}(N)\rho_{kj}(N) + \rho_{ki}(N)\rho_{jk}(N)}{\rho_{ij}(N)\rho_{kj}(N) + \rho_{ij}(N)\rho_{ki}(N) + \rho_{kj}(N)\rho_{ik}(N)}$.

From lemma 5, $m \leq N^{1/2} \exp(N\beta_{ji}) \, \rho_{ji}(N) \leq M$, so we can bound each of the six terms

in this ratio, for example

$m^2 \left(N \exp(N(\beta_{ji} + \beta_{ki})) \right)^{-1} \leq \rho_{ji}(N)\rho_{ki}(N) \leq M^2 \left(N \exp(N(\beta_{ji} + \beta_{ki})) \right)^{-1}$. Since all six

terms are positive, if $\gamma_i > \gamma_j$, $\lim_{N \to \infty} x_i^*(N) = 0$. ∎

As in the 2x2 case, a ½-dominant equilibrium need not be selected. The easiest

examples are where strategy 3 risk-dominates both strategy 1 and strategy 2 in pairwise

comparisons (so it is "pairwise risk dominant") but where strategy 1 or 2 is selected over

strategy 3 as $N \to \infty$ in the 2x2 games. This is the case in the following payoff matrix

where strategy 1 is selected, i.e. $\lim_{N \to \infty} x_1^*(N) = 1$:

$$
\begin{array}{ccc}
16 & 5 & 8 \\
1 & 16 & 8 \\
1 & 1 & 24
\end{array}
$$

5   Weak Selection

So far we have supposed that the payoff or fitness of an agent is entirely

determined by the fitness functions. We now return to the case of 2x2 games and that

earlier notation to investigate what happens if the fitness is the sum of a "game payoff"

and a "baseline fitness," and moreover selection is weak in the sense that the game makes

a small contribution to total payoff.

In the application of evolutionary dynamics to biology, it is natural to consider

the case of weak selection, as most genetic mutations lead to very small changes in the

phenotype or behavior of animals and consequently have only a very small effect on the fitness. Indeed the overwhelming majority of molecular mutations do not change fitness at all and are called 'neutral' mutations, and many results in population genetics are derived for the limit of weak selection or even neutrality.

It is also of interest to study weak selection in a social context. We are engaged in many different simultaneous games, and the outcome in any one of them might only have a small contribution to our overall success. Thus, it is very natural to assume that players have a baseline payoff and the particular game that is being considered provides only an incremental contribution to the total payoff. At the same time, it may be difficult for players to disentangle the factors that lead to the success of another agent, so that decisions about whose strategy to imitate in a given game might be based on overall fitness instead of on performance in the game at hand.

To study weak selection, we replace the assumption that

$$f_s = \big(a(s-1)+b(N-s)\big)/(N-1) \text{ and } g_s = \big(cs+d(N-s-1)\big)/(N-1) \text{ with}$$

$$f_s = 1-w+w\big(a(s-1)+b(N-s)\big)/(N-1) \text{ and } g_s = 1-w+w\big(cs+d(N-s-1)\big)/(N-1),$$

so that $w \in [0,1]$ measures the contribution of the game to overall fitness; $w = 1$ is our previous case, while $w = 0$ is the case of neutral selection.

The argument of lemma 3 still holds, and the nature of the long-run distribution is again determined by whether $\rho_{BA}/\rho_{AB} = \prod_{s=1}^{N-1} \dfrac{f_s}{g_s} \equiv \gamma$ is greater or less than $1/k$.

However, the form of the fitness functions has changed. Standard game-theoretic solution concepts such as best response and Nash equilibrium are unaffected by any affine, positively-sloped, transformation of the payoff functions, and this is also true for long-run predictions of the replicator dynamic, inspection of the formula for γ shows that it changes when payoffs are shifted by an additive constant. In particular, we can sharpen the conclusions of the last section for cases where w is sufficiently small, so that all of the payoffs are close to 1.

<u>Lemma 6</u>: For fixed N, $\gamma = \prod_{s=1}^{N-1} \dfrac{f_s}{g_s} = 1 + w\left(\dfrac{N}{2}(a+b-c-d)+d-a\right)+o(w).$

Proof: Using the approximation $1/(1+x)=1-x+o(x)$, we write

$$1/g_s = \dfrac{1}{1+w\left(\dfrac{cs+d(N-s-1)}{N-1}-1\right)} \approx 1-w\dfrac{cs+d(N-s-1)-(N-1)}{N-1}+o(w)$$

So

$$\dfrac{f_s}{g_s}=1+w\left(\dfrac{\big(a(s-1)+b(N-s)\big)-(N-1)}{N-1}\right)\left(1-w\left(\dfrac{cs+d(N-s-1)-(N-1)}{N-1}\right)\right)+o(w)$$

$$=1+w\left(\dfrac{\big(a(s-1)+b(N-s)\big)-(cs+d(N-s-1))}{N-1}\right)+o(w)$$

$$=1+w\left(\dfrac{\big(a-c+d-b\big)s+(N-1)(b-d)+(b-a)}{N-1}\right)+o(w).$$

Let $\alpha = a-c+d-b$, and let $\beta = (N-1)(b-d)+b-a$.

Then $\dfrac{f_s}{g_s}=1+w\dfrac{\alpha s+\beta}{N-1}+o(w)$, so

$$\gamma = \prod_{s=1}^{N-1}\dfrac{f_s}{g_s}=1+\dfrac{w}{N-1}(\alpha\dfrac{(N-1)N}{2}+(N-1)\beta)+o(w)$$

$$=1+w\left(\dfrac{N}{2}(a-c+d-b)+(N-1)(b-d)+b-a\right)+o(w)$$

$$=1+w\left(\dfrac{N}{2}(a+b-c-d)+d-a\right)+o(w). \qquad\blacksquare$$

<u>Corollary 2:</u> In a game where *(A, A)* and (B,B) are both Nash equilibria, the risk-dominant equilibrium is selected in the double limit $\lim_{N\to\infty}\lim_{w\to 0} x^*(k,N)$.

19

6.   Conclusion

Our analysis shows that the behavior of "replicator-like" systems in finite populations can be different than that of the standard replicator dynamic. The differences are most striking in the case of small populations, where the expected motion differs from that of the replicator, but even in large populations the asymptotic predictions of the two models can differ.

Appendix

Proof of Theorem 2 , case b.3

Our goal is to characterize the behavior of γ as $N \to \infty$, where

$$\gamma = \frac{((N-1)b)((N-2)b+a)....(b+(N-2)a)}{(c+(N-2)d)(2c+(N-3)d)...((N-2)c+d)((N-1)c)}$$

$$= \frac{d}{a}\frac{(N-1)a}{(N-1)d}\frac{\left(b+(N-2)a\right)...\left((N-2)b+a\right)\left((N-1)b\right)}{\left(c+(N-2)d\right)...\left((N-2)c+d\right)\left((N-1)c\right)}$$

$$= \frac{d}{a}\prod_{s=0}^{N-1}\left(\frac{aj+b(N-1-s)}{cj+d(N-1-s)}\right)$$

We will approach this by comparing the numerator of the expression to the denominator.

We rewrite the numerator as

$$d\prod_{s=0}^{N-1}\left[a\frac{s}{N-1}+b(1-\frac{s}{N-1})\right] = d\exp N\sum_{s=0}^{N-1}\left(\frac{1}{N}\right)\ln\left(a\frac{s}{N-1}+b(1-\frac{s}{N-1})\right), \text{ and}$$

the denominator as $a\prod_{s=0}^{N-1}\left[c\frac{s}{N-1}+d(1-\frac{s}{N-1})\right]$. We then approximate the

numerator by $d\exp\left(N\int_0^1\ln(a+(b-a)x)dx\right)+O(1)$, and the denominator by

$a\exp\left(N\int_0^1\ln(c+(d-c)x)dx\right)+O(1)$. For large N, this comparison is determined by the

comparison of the integrals, and γ converges to either 0 or infinity.

Since

$$\int\ln(a+(b-a)x)dx = x\ln(a+(b-a)x)-x+\frac{a}{b-a}\ln(a+(b-a)x),$$

$$\int_0^1\ln(a+(b-a)x)dx = \frac{b}{b-a}\ln b-\frac{a}{b-a}\ln a-1.$$

So the question becomes whether

$$\left(\frac{b\ln b - a\ln a}{b-a}\right) > \left(\frac{d\ln d - c\ln c}{d-c}\right).$$

$\blacksquare$

<u>Claim :</u> There are cases with $a+b<c+d$ but $\left(\dfrac{b\ln b - a\ln a}{b-a}\right) > \left(\dfrac{d\ln d - c\ln c}{d-c}\right)$.

Take c=1, $b=8, a=16, d=24$. Then the LHS= $5\ln 2 \approx 3.465$; the RHS=

$\dfrac{24\ln 24}{23} \approx 3.307$.

<u>Proof of lemma 5:</u> Fix a pair of distinct strategies i and j. From lemma 2,

$$\frac{1}{\rho_{ij}(N)} = 1 + \sum_{\nu=1}^{N-1}\prod_{\kappa=1}^{\nu}\frac{\kappa a_{ij} + (N-1-\kappa)a_{ii}}{(\kappa-1)a_{jj}+(N-\kappa)a_{ji}}$$

$$= 1 + \sum_{\nu=1}^{N-1}\frac{\nu a_{jj}+(N-1-\nu)a_{ji}}{(N-1)a_{ji}}\prod_{\kappa=1}^{\nu}\frac{\kappa a_{ij}+(N-1-\kappa)a_{ii}}{\kappa a_{jj}+(N-1-\kappa)a_{ji}}$$

$$= 1 + \sum_{\nu=1}^{N-1}\frac{\nu a_{jj}+(N-1-\nu)a_{ji}}{(N-1)a_{ji}}\exp\left\{\sum_{\kappa=1}^{\nu}\phi_{ij}\left(\frac{\kappa}{N-1}\right)\right\}. \qquad (2)$$

Set $\psi(\xi) = \int_0^\xi \phi_{ij}(z)dz$ and $K_1 = \sup\left\{\left|\phi'_{ij}(z)\right| : 0 \le z \le 1\right\}$. Since all payoffs are

positive, $K_1 < \infty$. Thus by the mean value theorem,

$$\phi_{ij}\left(\frac{\kappa}{N-1}\right) \le (N-1)\int_{(\kappa-1)/(N-1)}^{\kappa/(N-1)}\phi_{ij}(z)dz + \frac{K_1}{N-1} \text{ for } \kappa = 1,\ldots,N-1$$

and so, for $\nu = 1,\ldots,N-1$,

$$\exp\left\{\sum_{\kappa=1}^{\nu}\phi_{ij}\left(\frac{\kappa}{N-1}\right)\right\} \le \exp\left\{(N-1)\psi\left(\frac{\nu}{N-1}\right)+K_1\right\}.$$

The positivity of the payoffs also implies that ψ is Lipschitz continuous with

Lipschitz constant $K_2 = \sup\left\{\left|\phi_{ij}(z)\right| : 0 \le z \le 1\right\}$. Thus

$$\exp\left\{(N-1)\psi\left(\frac{\nu}{N-1}\right)\right\} = (N-1)\int_{(\nu-1)/(N-1)}^{\nu/(N-1)} \exp\left\{(N-1)\psi\left(\frac{\nu}{N-1}\right)\right\}d\xi$$

$$\leq e^{K_2}(N-1)\int_{(\nu-1)/(N-1)}^{\nu/(N-1)} \exp\left\{(N-1)\psi(\xi)\right\}d\xi$$

for $\nu = 1,\ldots,N-1$.

Note also that $\dfrac{\nu a_{jj} + (N-1-\nu)a_{ji}}{(N-1)a_{ji}} \leq \max\{a_{jj}/a_{ji},1\}$ for all $\nu = 1,2,\ldots N-1$.

Substituting into (*), it follows that

$$\frac{1}{\rho_{ij}(N)} \leq 1 + \max\left\{a_{jj}/a_{ji},1\right\}e^{K_1+K_2}(N-1)\int_0^1 \exp[(N-1)\psi(\xi)]d\xi$$

A similar argument shows that

$$\frac{1}{\rho_{ij}(N)} \geq 1 + \min\left\{a_{ij}/a_{ii},1\right\}e^{-K_1-K_2}(N-1)\int_0^1 \exp[(N-1)\psi(\xi)]d\xi$$

To determine the asymptotic behavior of the integral note that $\phi_{ij}(z) > 0$ for $0 \leq z < z_{ij}^*$ and $\phi_{ij}(z) < 0$ for $z_{ij}^* < z \leq 1$. Thus $\psi(\xi) < \psi(z_{ij}^*) = \beta_{ij}$ for all $\xi \neq z_{ij}^*$. Moreover, $\psi''(z_{ij}^*) = \phi_{ij}'(z_{ij}^*) < 0$. Thus the Laplace method for approximating integrals of the form $\int \exp(Nh(x))dx$ as $N \to \infty$ (see e.g. De Bruijn [1958], chapter 4) yields that

$$\lim_{N\to\infty} \frac{\int_0^1 \exp[N\psi(\xi)]d\xi}{N^{-1/2}\exp(N\beta_{ij})} = \sqrt{-\frac{2\pi}{\phi_{ij}'(z_{ij}^*)}}.$$

It follows that there exist constants $0 < m_{ij} < M_{ij} < \infty$ such that $m_{ij} \leq N^{1/2}\exp(N\beta_{ij})\rho_{ij}(N) \leq M_{ij}$ for all $N \geq 2$. The assertion is obtained by considering all pairs of distinct strategies and taking $m = \min_{i \neq j} m_{ij}$ and $M = \max_{i \neq j} M_{ij}$. ∎

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