

Stochastic Fluctuations through Intrinsic Noise in Evolutionary Game Dynamics*

Yi Tao

Key Laboratory of Animal Ecology and Conservation Biology
Institute of Zoology
Chinese Academy of Sciences
Beijing, China

Ross Cressman[†]

Department of Mathematics
Wilfrid Laurier University
Waterloo, Ontario, N2L 3C5
Canada

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[†]author for correspondence, e-mail: rcressma@wlu.ca

Abstract: A one-step (birth-death) process is used to investigate stochastic noise in an elementary two-phenotype evolutionary game model based on a payoff matrix. In this model, we assume that the population size is finite but not fixed and that all individuals have, in addition to the frequency-dependent fitness given by the evolutionary game, the same background fitness that decreases linearly in the total population size. Although this assumption guarantees population extinction is a globally attracting absorbing barrier of the Markov process, sample trajectories do not illustrate this result even for relatively small carrying capacities. Instead, the observed persistent transient behavior can be analyzed using steady state statistics of our model of intrinsic noise based on random pairwise interactions between individuals. It is shown that there is good agreement between the theory of these statistics and the simulation results. Furthermore, the ESS of the evolutionary game can be used to predict the mean steady state.

Keywords: intrinsic noise, ESS, evolutionary games, stochastic effects

Author for correspondence:
Ross Cressman
e-mail: rcressma@wlu.ca

Mailing address:
Department of Mathematics
Wilfrid Laurier University
Waterloo, Ontario, N2L 3C5
Canada

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1 Introduction

It is well known that one of the basic assumptions of standard evolutionary game theory developed by Maynard Smith (1982) (see also Taylor and Jonker (1978), Lessard (1984), Cressman (1992), Hofbauer and Sigmund (1998, 2003)) is that the population size is effectively infinite. In particular, the population size is sufficiently large so that stochastic effects can be ignored (Peck and Feldman, 1988) in the deterministic evolutionary dynamics based on expected payoffs through random pairwise interactions between individuals. However, for real populations, this assumption is not always valid, in which case stochastic effects due to finite populations (or other factors) may be important in the evolutionary outcome of the dynamics.

Consider the standard deterministic single-species game-theoretic model (see Section 2 below) where each individual is characterized by its phenotype (or strategy) and its fitness is a function of the population's phenotypic distribution through the game's payoff matrix. As pointed out by Foster and Young (1990), this model does not account for stochastic terms that may arise from a variety of factors. First, there is variability due to differences between an individual's realized and expected payoffs resulting from random interactions with other individuals. Second, there is natural variability in the payoff matrix that results from environmental influences. Third, there is background mutation, and possibly immigration of individuals from other gene pools.

Each of these stochastic factors have been examined under the assumption that the population size is finite and fixed. For instance, a great deal of research analyzing the effect of rare mutations began with Foster and Young (1990) who considered a particular case of what is now called a stochastically stable strategy. They showed that a stochastically stable strategy differs from both the traditional evolutionarily stable strategy (ESS) and the concept of an attractor in a deterministic dynamical system. More recently, Broom (2005) analyzed the effect of variable payoffs on the ESS. The model of Taylor et al. (2004) is more directly relevant for our approach since its assumptions of fixed payoff matrix and no mutation effects are the same as ours. Specifically, they analyzed stochastic evolutionary game dynamics with finite population size using a frequency-dependent Moran process (1962) that assumes: (1) The population size is a fixed constant; (2) At each time step, an individual is chosen for reproduction proportional to its fitness; (3) One identical offspring is produced which replaces another randomly chosen

individual (see also Fogel et al. (1997, 1998), Ficici and Pollack (2000)).

In this paper, we also investigate stochastic fluctuations in evolutionary game dynamics. However, although our population is finite, its size varies according to a one-step birth-death process (van Kampen, 1992) where, at each step, an individual either dies or reproduces an identical offspring. Thus, our process is closer to models of intrinsic noise as used in the physical sciences to predict the appearance and disappearance of different types of particles under random interactions (van Kampen, 1992). In our intrinsic noise model, particles are individuals exhibiting different strategies in the population and their numbers change according to their fitness (see Section 3 below). This approach to modelling stochastic fluctuations has gained recent interest in the biological literature (Swift, 2002; Tao, 2004; Tao et al., 2005) in other contexts as well.

In our model, species extinction is a globally attracting absorbing barrier of the Markov process but this is seldom observed in sample trajectories when the deterministic model has even a moderate equilibrium population size of 20 or more individuals. For this reason, we concentrate on analyzing the steady state statistics (i.e. the mean and variance) of the conditional distribution assuming the population does not go extinct. This is in contrast to the approach of Taylor et al. (2004) who focus instead on the conditions for selection to favor successful invasion and or/fixation of new phenotypes by calculating the corresponding barrier's absorption probability.

The basic evolutionary game model is from Maynard Smith (1982) but we assume that the individual's background fitness depends on the population size. Our main goal is to show how the population size affects the statistical properties of evolutionary game dynamics. The paper is organized as follows. In Section 2, the basic deterministic model for evolutionary game dynamics is briefly described and related to the static concept of an evolutionarily stable strategy. Section 3 develops our intrinsic noise model for the elementary two-phenotype matrix game model of Section 2. We then analyze this stochastic model when the equilibrium of the underlying deterministic system is monomorphic (Section 4) and when it is polymorphic (Section 5). The final section summarizes the results in relation to the ESS concept and the Appendix contains some of the longer proofs.

2 The Deterministic Model and Evolutionarily Stable Strategies

In order to clearly illustrate the effect of intrinsic noise on the evolutionary dynamics, we will apply it to the case of a single species where each individual uses one of two possible (pure) strategies, R_1 and R_2 . Suppose p_i is the proportion of the population using strategy R_i .

In the deterministic model, individuals interact in random pairwise contests and so those using strategy R_i receive an expected payoff of

$$f_i = \sum_{j=1}^2 a_{ij} p_j = e_i \cdot Ap \text{ for } i = 1, 2. \quad (1)$$

Here $A = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}$ is the 2×2 payoff matrix whose entry a_{ij} denotes the payoff to strategy (or phenotype) R_i when interacting with R_j , $p = (p_1, 1-p_1)$ is the frequency vector of strategy types in $\Delta^2 \equiv \{(p_1, p_2) : p_1 + p_2 = 1, p_i \geq 0\}$, e_i is the i th unit coordinate vector (e.g. $e_1 = (1, 0)$) corresponding to R_i , and $u \cdot Av \equiv \sum_{i,j=1}^2 u_i a_{ij} v_j$ is the standard inner product. We assume $a_{ij} \geq 0$ for all $1 \leq i, j \leq 2$. To include population size effects, we also assume the fitness of an individual using pure strategy R_i is given by

$$W_i = f_i + W_0$$

where W_0 is called the background fitness (Maynard Smith, 1982). That is, W_0 is the component of an individual's fitness that is not due to contests in the population. We assume that all individuals have the same background fitness which is given by

$$W_0(N) = 1 - \beta N$$

where N is the total population size and the positive parameter $1/\beta$ can be thought of as the environmental carrying capacity. In particular, background fitness depends only on the population size and is independent of the strategy type.

With fitness interpreted as the reproductive success of an individual (who produces offspring with the same strategy), the continuous-time deterministic dynamics becomes

$$\begin{aligned} \frac{dn_1}{dt} &= W_1 n_1 = n_1 (e_1 \cdot Ap + 1 - \beta N) \\ \frac{dn_2}{dt} &= W_2 n_2 = n_2 (e_2 \cdot Ap + 1 - \beta N) \end{aligned} \quad (2)$$

where $n_i = p_i N$ is the number of individuals with phenotype R_i . Following Lessard (1984), this can be rewritten in terms of N and p_1 as

$$\frac{dp_1}{dt} = p_1(1-p_1)(W_1 - W_2) = p_1(1-p_1)(e_1 \cdot Ap - e_2 \cdot Ap) \quad (3)$$

$$\frac{dN}{dt} = N\bar{W} \quad (4)$$

where $\bar{W} = p_1 W_1 + (1-p_1)W_2$ is the mean fitness of the population. Equation (3) is the replicator equation (Taylor and Jonker, 1978).

The equilibria (p^*, N^*) and their stability for the dynamics (3) (4) can be understood in terms of the ESS structure of the game with payoff matrix A as outlined in the following paragraph. First, notice that common background fitness implies the one-dimensional dynamics (3) is independent of N and so its evolutionary outcome p^* can be determined and then substituted into (4) to find N^* (Cressman, 1992). Furthermore, the equilibrium $N^* = 0$ is unstable due to our assumption that all payoffs are nonnegative.

According to Maynard Smith's (1982) definition, $S \in \Delta^2$ is an ESS if and only if for all $\hat{S} \in \Delta^2$ different from S ,

$$\text{either } (\hat{S} - S) \cdot AS < 0 \quad (5)$$

$$\text{or } (\hat{S} - S) \cdot AS = 0 \quad \text{and} \quad (\hat{S} - S) \cdot A\hat{S} > 0 \quad (6)$$

(Lessard, 1984; Cressman, 1992; Hofbauer and Sigmund, 1998). It is convenient to add 1 to all the payoff entries (that does not alter the ESS structure) and define $b_{ij} \equiv a_{ij} + 1$, $1 \leq i, j \leq 2$.

The monomorphic equilibrium with no individuals using strategy R_2 (i.e. the boundary point $(p^* = (1, 0), N^* = b_{11}/\beta)$) is locally asymptotically stable for (3) (4) if and only if $b_{11} > b_{21}$ if and only if this equilibrium is an ESS.¹ Likewise, $(p^* = (0, 1), N^* = b_{22}/\beta)$ is locally asymptotically stable if and only if $b_{22} > b_{12}$ if and only if this equilibrium is an ESS. If both these monomorphic equilibria are ESS's, then there is an unstable polymorphic

¹Here we ignore the degenerate possibility that $b_{11} = b_{21}$ (in which case we would also need to compare b_{12} to b_{22}). We also assume $b_{12} \neq b_{22}$.

equilibrium (i.e. p^* is in the interior of Δ^2) that is not an ESS given by

$$p_1^* = \frac{b_{12} - b_{22}}{b_{12} - b_{22} + b_{21} - b_{11}} \quad (7)$$

$$N^* = \frac{1}{\beta} \frac{b_{12}b_{21} - b_{11}b_{22}}{b_{12} - b_{22} + b_{21} - b_{11}}. \quad (8)$$

This equilibrium separates the domain of attraction of the boundary ESS's. If exactly one monomorphic equilibrium is an ESS, it is globally asymptotically stable (and so there is no interior equilibrium). Finally, if neither monomorphic equilibrium is an ESS, the interior equilibrium (7) is an ESS and globally asymptotically stable.

3 Intrinsic Noise

Intrinsic noise is one of the most important stochastic processes in physics and chemistry. It is used there to describe the internal noise that is due to the system consisting of discrete particles (van Kampen, 1992) by modelling stochastic effects as a one-step (birth-death) process. In the context of evolutionary games, we interpret each individual as a particle in the system. Thus, with this interpretation, the theory of one-step (birth-death) processes can be used to investigate stochastic noise due to random interactions between individuals. We begin with a short description about this process as it applies to intrinsic noise in evolutionary games with finite population size.

Let $\Phi(n_1, n_2; t)$ denote the joint probability distribution that the numbers of R_1 and R_2 equal n_1 and n_2 at time t . As a one-step process, $\Phi(n_1, n_2; t)$ may jump to an adjacent state $n_1 \pm 1$ or $n_2 \pm 1$ in the time interval Δt with probability proportional to individual fitness. $\Phi(0, 0; t)$ is then an increasing function of t since $(n_1, n_2) = (0, 0)$ is an absorbing barrier. Moreover, every trajectory of this stochastic process will eventually be absorbed at $(n_1, n_2) = (0, 0)$ (i.e. $(n_1, n_2) = (0, 0)$ is a globally absorbing steady state) (see the following section).

Here, it is assumed that Δt is sufficiently small that at most one birth-death event occurs during this time interval (Swift, 2002). From (2), the probability that n_i increases to $n_i + 1$ is $b_i n_i \Phi(n_1, n_2; t) \Delta t$ where $b_i \equiv e_i \cdot Ap + 1 = p_1 b_{i1} + p_2 b_{i2}$ and that n_i decreases to $n_i - 1$ is $n_i \beta N \Phi(n_1, n_2; t) \Delta t$

where $N = n_1 + n_2$. That is,

$$\begin{aligned} \frac{\Phi(n_1, n_2; t + \Delta t) - \Phi(n_1, n_2; t)}{\Delta t} &= (n_1 + 1) \beta(N + 1) \Phi(n_1 + 1, n_2; t) - n_1 \beta N \Phi(n_1, n_2; t) \\ &\quad + (n_2 + 1) \beta(N + 1) \Phi(n_1, n_2 + 1; t) - n_1 \beta N \Phi(n_1, n_2; t) \\ &\quad + b_1 (n_1 - 1) \Phi(n_1 - 1, n_2; t) - b_1 n_1 \Phi(n_1, n_2; t) \\ &\quad + b_2 (n_2 - 1) \Phi(n_1, n_2 - 1; t) - b_2 n_2 \Phi(n_1, n_2; t) \\ &= \sum_{i=1}^2 ((E_i^{+1} - 1) \beta N n_i \Phi + (E_i^{-1} - 1) b_i n_i \Phi) \end{aligned} \quad (9)$$

where $E_i^{\pm 1}$ is the operator given by $E_i^{\pm 1} g(n_1, n_2) = \begin{cases} g(n_1 \pm 1, n_2) & \text{if } i = 1 \\ g(n_1, n_2 \pm 1) & \text{if } i = 2 \end{cases}$ that shifts the population of species i by one individual.

Thus, the master equation of $\Phi(n_1, n_2; t)$ corresponding to (2) (van Kampen, 1992) in continuous time is given by

$$\frac{\partial \Phi(n_1, n_2; t)}{\partial t} = \sum_{i=1}^2 ((E_i^{+1} - 1) \beta N n_i \Phi + (E_i^{-1} - 1) b_i n_i \Phi). \quad (10)$$

Clearly, $(n_1, n_2) = (0, 0)$ remains an absorbing barrier of this continuous-time Markov process. We are more interested in the transient behavior of sample trajectories for the Markov process that is based on the conditional probability distribution of $\Phi(n_1, n_2; t)$ that assumes the population does not go extinct (i.e. either $n_1 \neq 0$ or $n_2 \neq 0$ or both). In particular, we approximate the evolution of the mean and variance of this conditional distribution by expanding the operators $E_i^{\pm 1}$ about equilibrium points (p^*, N^*) of the deterministic dynamics when p^* is either on the boundary (Section 4) or the interior (Section 5) of Δ^2 .

4 Intrinsic Noise for Boundary Equilibria

The theory of intrinsic noise is most straightforward when all individuals in the population are using the same strategy, say R_1 . For the deterministic model, the dynamics (2) is now one-dimensional (since $n_2(t) = 0$ for all t) given by $\dot{n}_1 = n_1 (a_{11} + 1 - \beta n_1) = n_1 (b_{11} - \beta n_1)$ with globally asymptotically stable equilibrium $n_1^* = b_{11}/\beta$ corresponding to the boundary equilibrium $(p^* = (1, 0), N^* = b_{11}/\beta)$. We develop the corresponding model with

intrinsic noise in the following section before returning to examine intrinsic noise near $(p^* = (1, 0), N^* = b_{11}/\beta)$ in the full dynamical system (2) in Section 4.2.

4.1 Internal Steady State Statistics

In this section, we assume that $n_2 = 0$ initially (and so, from (9), $n_2 = 0$ for all time) and denote the probability distribution $\Phi(n_1, 0; t)$ that the number of R_1 individuals equals n_1 at time t by $\Phi(n_1; t)$ for convenience. Suppose, on average, one individual gives birth (to an offspring also using R_1) or dies per unit time with relative probabilities $n_1 b_{11}$ and βn_1^2 respectively.

Clearly, $n_1 = 0$ is an absorbing barrier of this discrete-time Markov process. Moreover, by Appendix A, every trajectory of this stochastic process will eventually be absorbed at $n_1 = 0$ (i.e., $n_1 = 0$ is a globally absorbing steady state). For instance, in Figure 1a where $\beta = 1$ and $a_{11} = 3$, the equilibrium size for the monomorphic population using strategy R_1 is $n_1^* = 4$. We see that within 200 time steps the population has gone extinct for the sample path depicted. However, from Figure 1bc with $\beta = .1$ and $\beta = .01$ respectively (i.e. $n_1^* = 40$ and $n_1^* = 400$ respectively), there is no indication the population will go extinct for these sample paths even after 40,000 time steps. In fact, from simulations, observed sample paths rarely go extinct for moderate equilibrium sizes of $n_1^* \cong 20$.

Figure 1 about here

Let us assume that the equilibrium population size is large enough (e.g. $n_1^* \geq 20$) so that we do not expect populations to go extinct along observed sample paths. We are then more interested in the transient behavior of the sample paths which we investigate by making the following two approximations to (9).

First, the master equation (10) of $\Phi(n_1, 0; t)$ corresponding to (9) (cf. (2)) is now

$$\frac{\partial \Phi(n_1; t)}{\partial t} = (E_1^{+1} - 1) \beta n_1^2 \Phi + (E_1^{-1} - 1) b_{11} n_1 \Phi \quad (11)$$

where the step operator is $E_1^{\pm 1} g(n_1) = g(n_1 \pm 1)$. Notice that the Taylor expansion of the step operator $E_1^{\pm 1}$ is

$$E_1^{\pm 1} = 1 \pm \frac{\partial}{\partial n_1} + \frac{1}{2} \frac{\partial^2}{\partial n_1^2} \pm \frac{1}{3!} \frac{\partial^3}{\partial n_1^3} + \dots$$

(van Kampen, 1992). Hence, omitting all derivatives beyond second order, the Fokker-Planck approximation of the master equation is

$$\frac{\partial \Phi(n_1; t)}{\partial t} = -\frac{\partial}{\partial n_1} (b_{11} - \beta n_1) n_1 \Phi + \frac{1}{2} \frac{\partial^2}{\partial n_1^2} (b_{11} + \beta n_1) n_1 \Phi. \quad (12)$$

Clearly, from Figure 1, sample trajectories of (9) remain bounded. For this reason, we look for solutions $\Phi(n_1; t)$ of (12) that evolve to 0 rapidly as $n_1 \rightarrow \infty$. For example, we take boundary conditions here as $\lim_{n_1 \rightarrow \infty} \Phi(n_1; t) = 0$, $\lim_{n_1 \rightarrow \infty} n_1 \Phi(n_1; t) = 0$, $\lim_{n_1 \rightarrow \infty} \frac{\partial \Phi(n_1; t)}{\partial n_1} = 0$ etc (and $\Phi(n_1; t) = 0$ if n_1 is negative).

The steady state statistics (van Kampen, 1992) at the boundary equilibrium $n_1^* = \frac{b_{11}}{\beta}$ refer to the mean and variance of the following approximation of (12). When n_1 is near this equilibrium n_1^* , let $x_1 \equiv n_1 - n_1^*$. By expanding $(b_{11} - \beta n_1) n_1$ and $(b_{11} + \beta n_1) n_1$ from (12) in terms of x and retaining only the lowest non-zero terms, we obtain

$$\frac{\partial \Phi(x_1; t)}{\partial t} = b_{11} \frac{\partial}{\partial x} x_1 \Phi + \frac{b_{11}^2}{\beta} \frac{\partial^2}{\partial x_1^2} \Phi. \quad (13)$$

Let $\langle x_1 \rangle \equiv \int_{-\infty}^{\infty} x_1 \Phi(x_1; t) dx_1$ $\langle x_1^2 \rangle \equiv \int_{-\infty}^{\infty} x_1^2 \Phi(x_1; t) dx_1$ be the first and second moments of a solution $\Phi(x_1; t)$ of (13). Since there is no a priori reason $n_1 \geq 0$ (i.e. $x_1 \geq -n_1^*$) in this approximation, we allow $n_1 \rightarrow \pm\infty$ and replace the boundary conditions of (12) by $\lim_{n_1 \rightarrow \pm\infty} \Phi(n_1; t) = 0$, $\lim_{n_1 \rightarrow \pm\infty} n_1 \Phi(n_1; t) = 0$, $\lim_{n_1 \rightarrow \pm\infty} \frac{\partial \Phi(n_1; t)}{\partial n_1} = 0$ etc. Thus

$$\begin{aligned} \frac{d \langle x_1 \rangle}{dt} &= \int_{-\infty}^{\infty} x_1 \frac{\partial \Phi(x_1; t)}{\partial t} dx_1 = \int_{-\infty}^{\infty} x_1 \left(b_{11} \frac{\partial}{\partial x_1} x_1 \Phi + \frac{b_{11}^2}{\beta} \frac{\partial^2}{\partial x_1^2} \Phi \right) dx_1 \\ &= b_{11} x_1^2 \Phi \Big|_{-\infty}^{\infty} - b_{11} \int_{-\infty}^{\infty} x_1 \Phi dx_1 + \frac{b_{11}^2}{\beta} \left[x_1 \frac{\partial \Phi}{\partial x_1} \Big|_{-\infty}^{\infty} - \int_{-\infty}^{\infty} \frac{\partial \Phi}{\partial x_1} dx_1 \right] \\ &= -b_{11} \langle x_1 \rangle \\ \frac{d \langle x_1^2 \rangle}{dt} &= \int_{-\infty}^{\infty} x_1^2 \frac{\partial \Phi(x_1; t)}{\partial t} dx_1 = \int_{-\infty}^{\infty} x_1^2 \left(b_{11} \frac{\partial}{\partial x_1} x_1 \Phi + \frac{b_{11}^2}{\beta} \frac{\partial^2}{\partial x_1^2} \Phi \right) dx_1 \\ &= b_{11} \left[x_1^3 \Phi \Big|_{-\infty}^{\infty} - \int_{-\infty}^{\infty} 2x_1^2 \Phi dx_1 \right] + \frac{b_{11}^2}{\beta} \left[x_1^2 \frac{\partial \Phi}{\partial x_1} \Big|_{-\infty}^{\infty} - \int_{-\infty}^{\infty} 2x_1 \frac{\partial \Phi}{\partial x_1} dx_1 \right] \\ &= -2b_{11} \langle x_1^2 \rangle - \frac{2b_{11}^2}{\beta} \left[- \int_{-\infty}^{\infty} \Phi dx_1 \right] \\ &= -2b_{11} \langle x_1^2 \rangle + \frac{2b_{11}^2}{\beta}. \end{aligned}$$

That is, $\langle x_1 \rangle$ and $\langle x_1^2 \rangle$ evolve to 0 and $\frac{b_{11}}{\beta}$ respectively under (13). In fact, for large t , $\Phi(x_1; t)$ is a standard normal distribution with mean 0 and variance $\frac{b_{11}}{\beta}$ (van Kampen, 1992). Thus, for large t , the expectation and variance of n_1 near the equilibrium n_1^* are $\langle n_1 \rangle = \sigma_{n_1}^2 = \frac{b_{11}}{\beta}$. These are called the steady state statistics of the dynamics (12) for the equilibrium n_1^* .

Since these theoretical steady state statistics are based on two successive approximations of the one-step process (9), an immediate question is how accurate they are for the original equation. A naive test is to consider the mean and variance of the sample trajectories with 40,000 data points in Figure 1bc (i.e. when the population does not go extinct). For $\beta = 0.1$ (Figure 1b), the mean and variance are 39.675 and 39.695 respectively and for $\beta = 0.01$ (Figure 1c) they are 395.458 and 396.012.² These are consistent with the theoretical values of 40 (Figure 1b) and 400 (Figure 1c), especially given that the linearized terms in x become less accurate as variance increases.

To test this accuracy further, we performed Monte Carlo simulations following Gillespie (1997) for (11) using the payoff matrix $\begin{bmatrix} 3 & 1 \\ 1 & 3 \end{bmatrix}$ that has $b_{11} = 4$. As we can see from Figure 2, there is surprisingly good agreement for the means and variances (for the range of values $\beta = 0.01$ to 0.09). Although not apparent from Figure 2, it is clear from Figure 1 that the relative fluctuation strength $\sigma_{n_1} / \langle x_1 \rangle$ (defined by the coefficient of variation which is given by the standard deviation divided by the mean) decreases as $n_1^* = \frac{b_{11}}{\beta}$ increases. These results are also related to the concept of Fano factor (Thattai and van Oudenaarden, 2001; Tao, 2004; Tao et al., 2005) which is always 1 for our model.

Figure 2 about here

4.2 External Steady State Statistics - Is it possible that a mutant strategy can invade the population through intrinsic noise?

The question we examine in this section is whether the distribution of individuals using pure strategy R_1 found in Section 4.1 through internal in-

²Even for $\beta = 1$ (Figure 1a), the mean and variance are 4.456 and 3.049 for the first 180 time steps (i.e. before the population goes extinct) and these are reasonably consistent with the theoretical values of 4.

trinsic noise can be successfully invaded by a mutant strategist using pure strategy R_2 . For the deterministic system (2) (or equivalently (3) (4)), $(p^* = (1, 0), N^* = b_{11}/\beta)$ is asymptotically stable if and only if $b_{11} > b_{21}$ if and only if $p^* = (1, 0)$ is an ESS.

For this equilibrium, $n_1^* = \frac{b_{11}}{\beta}$ and $n_2^* = 0$. Let $x_1 = n_1 - n_1^*$ and $x_2 = n_2$. By using the same methods as in Section 4.1 (for details see Section 5 below), we obtain

$$\frac{d}{dt} \begin{pmatrix} \langle x_1 \rangle \\ \langle x_2 \rangle \end{pmatrix} = \begin{pmatrix} -b_{11} & b_{12} \\ 0 & b_{21} - b_{11} \end{pmatrix} \begin{pmatrix} \langle x_1 \rangle \\ \langle x_2 \rangle \end{pmatrix} \quad (14)$$

as the linear approximation to the master equation (10) for the evolution of the expected values of x_1 and x_2 . We see that $\langle x_1 \rangle$ and $\langle x_2 \rangle$ evolve to 0 if and only if $b_{11} > b_{21}$. That is, $n_1^* = \frac{b_{11}}{\beta}$ and $n_2^* = 0$ is asymptotically stable if and only if $p^* = (1, 0)$ is an ESS. This agrees with the simulation results of Figure 3 for the one-step process (9). That is, in Figure 3a where the payoff matrix is $\begin{bmatrix} 3 & 1 \\ 1 & 3 \end{bmatrix}$ with ESS $p^* = (1, 0)$, the simulations show R_2 cannot invade R_1 when the initial proportion of R_2 individuals are small (up to 10 percent in these simulations). On the other hand, when the payoff matrix is $\begin{bmatrix} 1 & 3 \\ 3 & 1 \end{bmatrix}$, there is no ESS at $p^* = (1, 0)$ and Figure 3b confirms R_2 does successfully invade R_1 since the proportion of R_2 individuals is increasing initially (as the population evolves towards the ESS $p^* = (\frac{1}{2}, \frac{1}{2})$). This latter situation is examined more closely in the following section.

Figure 3 about here

5 Intrinsic Noise for Interior Equilibria

We begin this section by giving the technical details of the linear expansion for the means and variances under the master equation. By omitting all derivatives beyond the second in the Taylor expansion $E_i^{\pm 1} = 1 \pm \frac{\partial}{\partial n_i} + \frac{1}{2} \frac{\partial^2}{\partial n_i^2} \pm \frac{1}{3} \frac{\partial^3}{\partial n_i^3} + \dots$ of the step operators $E_i^{\pm 1}$, the Fokker-Planck approximation of the master equation (10) is now (cf. (12))

$$\frac{\partial \Phi(n_1, n_2; t)}{\partial t} = \sum_{i=1}^2 \left(-\frac{\partial}{\partial n_i} (b_i - \beta N) n_i \Phi + \frac{1}{2} \frac{\partial^2}{\partial n_i^2} (b_i + \beta N) n_i \Phi \right) \quad (15)$$

When the system (3), (4) is near the interior (i.e. polymorphic) equilibrium (p^*, N^*) given by (7) and (8), we are interested in the steady-state statistics of (15). For this purpose, set $x_i = n_i - n_i^*$ ($i = 1, 2$), substitute this in (15), and expand the coefficients in powers of x_i . By retaining only the lowest non-zero terms, we obtain

$$\frac{\partial \Phi(x_1, x_2; t)}{\partial t} = \sum_{i=1}^2 \left(-\frac{\partial}{\partial x_i} (c_{i1}x_1 + c_{i2}x_2) \Phi + D_i \frac{\partial^2 \Phi}{\partial x_i^2} \right) \quad (16)$$

where $D_i \equiv \beta N^* n_i^*$ and $c_{ij} = \frac{\partial}{\partial n_j} (b_i - \beta N) n_i$ and these partial derivatives are evaluated at the equilibrium.³ That is

$$\begin{aligned} c_{11} &= \left((b_{11} - b_{12}) \frac{p_2^*}{N^*} - \beta \right) n_1^* & c_{12} &= - \left((b_{11} - b_{12}) \frac{p_1^*}{N^*} - \beta \right) n_1^* \\ c_{21} &= \left((b_{21} - b_{22}) \frac{p_2^*}{N^*} - \beta \right) n_2^* & c_{22} &= - \left((b_{21} - b_{22}) \frac{p_1^*}{N^*} + \beta \right) n_2^*. \end{aligned}$$

Using the zero boundary conditions

$$\lim_{x_1, x_2 \rightarrow \pm\infty} \Phi(x_1, x_2; t) = 0, \quad \lim_{x_1, x_2 \rightarrow \pm\infty} x_i \Phi(x_1, x_2; t) = 0, \quad \lim_{x_1, x_2 \rightarrow \pm\infty} \frac{\partial \Phi(x_1, x_2; t)}{\partial x_i} \text{ etc.}$$

³At the boundary equilibrium of Section 4.2, it is easy to verify that $c_{11} = -b_{11}$, $c_{12} = b_{12}$, $c_{21} = 0$, and $c_{22} = b_{21} - b_{11}$. This leads to (14) by following the same calculations that produce (17) at an interior equilibrium.

for $i = 1, 2$, we obtain

$$\begin{aligned}
\frac{d\langle x_1 \rangle}{dt} &= \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x_1 \frac{\partial \Phi}{\partial t} dx_1 dx_2 \\
&= \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x_1 \left(-\frac{\partial}{\partial x_1} (c_{11}x_1 + c_{12}x_2) \Phi + D_1 \frac{\partial^2 \Phi}{\partial x_1^2} \right) dx_1 dx_2 \\
&\quad + \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x_1 \left(-\frac{\partial}{\partial x_2} (c_{21}x_1 + c_{22}x_2) \Phi + D_2 \frac{\partial^2 \Phi}{\partial x_2^2} \right) dx_1 dx_2 \\
&= \int_{-\infty}^{\infty} \left[x_1 \left(- (c_{11}x_1 + c_{12}x_2) \Phi + D_1 \frac{\partial \Phi}{\partial x_1} \right) \right] \Big|_{x_1=-\infty}^{x_1=\infty} dx_2 \\
&\quad - \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \left(- (c_{11}x_1 + c_{12}x_2) \Phi + D_1 \frac{\partial \Phi}{\partial x_1} \right) dx_1 dx_2 \\
&\quad + \int_{-\infty}^{\infty} x_1 \left(- (c_{21}x_1 + c_{22}x_2) \Phi + D_2 \frac{\partial \Phi}{\partial x_2} \right) \Big|_{x_2=-\infty}^{x_2=\infty} dx_1 \\
&= c_{11} \langle x_1 \rangle + c_{12} \langle x_2 \rangle - \int_{-\infty}^{\infty} D_1 \Phi \Big|_{x_1=-\infty}^{x_1=\infty} dx_2 \\
&= c_{11} \langle x_1 \rangle + c_{12} \langle x_2 \rangle.
\end{aligned}$$

This combines with a similar calculation for $\frac{d\langle x_2 \rangle}{dt}$ to yield

$$\frac{d}{dt} \begin{pmatrix} \langle x_1 \rangle \\ \langle x_2 \rangle \end{pmatrix} = \begin{pmatrix} c_{11} & c_{12} \\ c_{21} & c_{22} \end{pmatrix} \begin{pmatrix} \langle x_1 \rangle \\ \langle x_2 \rangle \end{pmatrix}. \quad (17)$$

A straightforward calculation shows that $c_{11} + c_{22} = (b_{11} - b_{12} + b_{22} - b_{21}) p_1^* p_2^* - \beta N^* = \frac{2b_{12}b_{21} - b_{22}b_{21} - b_{12}b_{11}}{b_{11} - b_{12} + b_{22} - b_{21}} < 0$ for any interior equilibrium (p^*, N^*) . Thus, $(\langle x_1 \rangle, \langle x_2 \rangle) = (0, 0)$ is asymptotically stable for (17) if and only if $c_{11}c_{22} - c_{12}c_{21} = -\beta p_1^* p_2^* N^* (b_{11} - b_{12} + b_{22} - b_{21}) > 0$ if and only if the fixed interior equilibrium of (3), (4) is globally asymptotically stable (i.e. p^* is an ESS). In this case, the expectations of n_1 and n_2 evolve to $\langle n_1 \rangle = p_1^* N^*$ and $\langle n_2 \rangle = p_2^* N^*$, respectively. On the other hand, if p^* is not an ESS, then (p^*, N^*) is unstable and we expect the population to evolve to one of the boundary equilibria of Section 4. For this reason, we assume p^* is an ESS for the remainder of this section.

In order that (16) is a good approximation of the master equation (10), it is important that the distribution $\Phi(n_1, n_2; t)$ is not too spread out from the equilibrium $n_i^* = p_i^* N^*$. That is, we need to analyze the variance and covariance of solutions of (16). To this end, $\frac{d\langle x_i^2 \rangle}{dt} = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x_i^2 \frac{\partial \Phi}{\partial t} dx_1 dx_2 =$

$2c_{i1} \langle x_i x_1 \rangle + 2c_{i2} \langle x_i x_2 \rangle + 2D_i$ and $\frac{d\langle x_1 x_2 \rangle}{dt} = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x_1 x_2 \frac{\partial \Phi}{\partial t} dx_1 dx_2 = c_{21} \langle x_1^2 \rangle + (c_{11} + c_{22}) \langle x_1 x_2 \rangle + c_{12} \langle x_2^2 \rangle$ as shown in Appendix B. This is given in matrix form by

$$\frac{d}{dt} \begin{pmatrix} \langle x_1^2 \rangle \\ \langle x_1 x_2 \rangle \\ \langle x_2^2 \rangle \end{pmatrix} = \begin{pmatrix} 2c_{11} & 2c_{12} & 0 \\ c_{21} & c_{11} + c_{22} & c_{12} \\ 0 & 2c_{21} & 2c_{22} \end{pmatrix} \begin{pmatrix} \langle x_1^2 \rangle \\ \langle x_1 x_2 \rangle \\ \langle x_2^2 \rangle \end{pmatrix} + \begin{pmatrix} 2D_1 \\ 0 \\ 2D_2 \end{pmatrix}. \quad (18)$$

It is also shown in Appendix B that a (globally) asymptotically stable equilibrium for (18) exists with values

$$\begin{pmatrix} \langle x_1^2 \rangle \\ \langle x_1 x_2 \rangle \\ \langle x_2^2 \rangle \end{pmatrix} = \frac{1}{(c_{11} + c_{22})(c_{11}c_{22} - c_{12}c_{21})} \begin{pmatrix} -(c_{11} + c_{22})c_{22}D_1 - c_{12}(c_{12}D_2 - c_{21}D_1) \\ c_{11}c_{12}D_2 + c_{21}c_{22}D_1 \\ -(c_{11} + c_{22})c_{11}D_2 - c_{21}(c_{21}D_1 - c_{12}D_2) \end{pmatrix}$$

if and only if p^* is an ESS.

Since $\langle x_i \rangle = 0$ at equilibrium, these equilibrium values are the (co)variances of the joint distribution $\Phi(n_1, n_2; t)$ for large t as well. That is,

$$\begin{aligned} \sigma_{n_1}^2 &= -\frac{D_1(c_{11}c_{22} - c_{12}c_{21}) + D_1c_{22}^2 + D_2c_{12}^2}{(c_{11} + c_{22})(c_{11}c_{22} - c_{12}c_{21})} \\ &= -\frac{\beta(N^*)^2(p_1^*(c_{11}c_{22} - c_{12}c_{21}) + p_1^*c_{22}^2 + p_2^*c_{12}^2)}{(c_{11} + c_{22})(c_{11}c_{22} - c_{12}c_{21})} \\ \sigma_{n_2}^2 &= -\frac{D_2(c_{11}c_{22} - c_{12}c_{21}) + D_2c_{11}^2 + D_1c_{21}^2}{(c_{11} + c_{22})(c_{11}c_{22} - c_{12}c_{21})} \\ &= -\frac{\beta(N^*)^2(p_2^*(c_{11}c_{22} - c_{12}c_{21}) + p_2^*c_{11}^2 + p_1^*c_{21}^2)}{(c_{11} + c_{22})(c_{11}c_{22} - c_{12}c_{21})} \\ cov(n_1, n_2) &= \frac{D_1c_{21}c_{22} + D_2c_{11}c_{12}}{(c_{11} + c_{22})(c_{11}c_{22} - c_{12}c_{21})} \\ &= \frac{\beta(N^*)^2(p_1^*c_{21}c_{22} + p_2^*c_{11}c_{12})}{(c_{11} + c_{22})(c_{11}c_{22} - c_{12}c_{21})}. \end{aligned}$$

Since $c_{ij}, \beta N^*, p_1^*$ and p_2^* are all independent of β , we see that $\langle n_1 \rangle$ and $\langle n_2 \rangle$ as well as $\sigma_{n_1}^2, \sigma_{n_2}^2, cov(n_1, n_2)$ all grow linearly with respect to N^* (i.e. with respect to $1/\beta$) just as was the case for the steady state statistics of the stable boundary equilibria of Section 4.

On the other hand, for deterministic evolutionary game dynamics, we are often more interested in the phenotypic frequency of any interior stable

equilibrium. Thus, the steady state statistics of this frequency is also of interest under stochastic fluctuations. To calculate these, notice that p_1 can be approximated as

$$\begin{aligned} p_1 - p_1^* &= \frac{\partial}{\partial n_1} \left(\frac{n_1}{n_1 + n_2} \right) \Big|_{(n_1^*, n_2^*)} (n_1 - n_1^*) + \frac{\partial}{\partial n_2} \left(\frac{n_1}{n_1 + n_2} \right) \Big|_{(n_1^*, n_2^*)} (n_2 - n_2^*) \\ &= \frac{p_2^*}{N^*} (n_1 - n_1^*) - \frac{p_1^*}{N^*} (n_2 - n_2^*) \end{aligned}$$

if the system state is near the stable fixed point (p^*, N^*) . This approximation implies that the steady-state statistics of the frequency p_1 are

$$\begin{aligned} \langle p_1 \rangle &= p_1^* + \frac{p_2^*}{N^*} (\langle n_1 \rangle - n_1^*) - \frac{p_1^*}{N^*} (\langle n_2 \rangle - n_2^*) = p_1^* \\ \sigma_{p_1}^2 &= \frac{1}{(N^*)^2} ((p_2^*)^2 \sigma_{n_1}^2 + (p_1^*)^2 \sigma_{n_2}^2 - 2p_1^* p_2^* \text{cov}(n_1, n_2)) \\ &= -\frac{\beta}{(c_{11} + c_{22})(c_{11}c_{22} - c_{12}c_{21})} \left(\frac{(p_1^* p_2^*)(c_{11}c_{22} - c_{12}c_{21}) + (p_2^*)^2 (p_1^* c_{22}^2 + p_2^* c_{12}^2)}{+ (p_1^*)^2 (p_2^* c_{11}^2 + p_1^* c_{21}^2) + 2p_1^* p_2^* (p_1^* c_{21}c_{22} + p_2^* c_{11}c_{12})} \right) \\ &= \frac{\beta}{b_{12} - b_{22} + b_{21} - b_{11}} \\ &= \frac{\beta}{a_{12} - a_{22} + a_{21} - a_{11}} \end{aligned}$$

This result shows clearly that, for a given two-phenotype payoff matrix with $a_{12} > a_{22}$ and $a_{21} > a_{11}$, the variance of phenotypic frequency p_1 is a simple linear function of the parameter β , and it will decrease as β decreases (i.e. as the equilibrium population size N^* increases). That is, stochastic fluctuations are expected to become negligible for the frequency dynamics as population size becomes large and so the deterministic model can be used instead.

For a simple example, a comparison between the Monte Carlo simulations of (10) (the simulation algorithm is from Gillespie (1977)) and the theoretical predictions of the steady state predictions from (16) for different values of the parameter β is plotted in Figure 4 where the payoff matrix is given by $(a_{ij})_{2 \times 2} = \begin{bmatrix} 3 & 1 \\ 1 & 3 \end{bmatrix}$. This figure again shows that the theoretical analysis is quite accurate.

Figure 4 about here

6 Conclusion

In this paper, stochastic noise in a simple evolutionary game dynamics with two phenotypes is analyzed using the theory of one-step birth-death processes. We assume that the population size is finite but not fixed, and we mainly focus our attention on the statistics based on random interactions between individuals. This differs from other studies (e.g. Taylor et. al., 2004) of stochastic effects due to finite populations in evolutionary game theory where population size is assumed to be fixed. Moreover, this literature typically examines the long-term steady-state solution of the Markov process which, in our case, is of little interest since fitnesses that decrease in population size (i.e. logistic density effects) imply the population goes extinct (i.e. the only steady state is the trivial solution $n_1 = n_2 = 0$). Instead, we examine the transient behavior (that assumes the population is not extinct) which can be quite long lasting (see Figure 1bc) for even moderate equilibrium population sizes of 40 individuals in the corresponding deterministic model. Since these transient probability distributions are analytically intractable for our one-step process, we approximate their steady-state statistics (i.e. their means and variances) through linearizing the master equation of the associated continuous-time process. We find good agreement between these latter analytic statistics and simulation results of the original one-step process (see Figures 2 and 4).

Our main results show that the deterministic model of evolutionary game theory continues to predict the stochastic population means and that the stochastic effects on the variances become less important as the equilibrium population size increases. For two phenotypes with individual fitness given as a combination of pairwise interactions (through a payoff matrix) and a background fitness that is independent of phenotype, the deterministic model is fully understood by examining the ESS's of the payoff matrix. In particular, the frequencies of the two phenotypes approach the ESS proportions as the population size evolves to the N^* where logistic density effects exactly cancel the payoffs gained through pairwise interactions (Section 2). The same stable equilibrium occurs for the linearized master equation. Furthermore, stable equilibrium variances for the number of individuals using the two phenotypes can also be determined for this stochastic equation. In fact, these variances increase linearly in the equilibrium population size N^* . Thus, for large N^* , the frequency variance approaches zero. That is, stochastic effects become less and less relevant for large populations and only the deterministic model

of evolutionary game theory need be considered to model the evolution of phenotypic frequencies.

7 Appendix A

Here we show that every trajectory in Section 4.1 is eventually absorbed in the extinction state. A similar approach shows this is also true for the trajectories that start in the interior of the state space as in Sections 4.2 and 5. By the Mean Ergodic Theorem for discrete-time Markov processes (Bharucha-Reid, 1960),

$$\pi_{ij} \equiv \lim_{n \rightarrow \infty} \frac{1}{n} \sum_{\nu=0}^n p_{ij}^{(\nu)}$$

exists for all $0 \leq i, j < \infty$ and satisfies $\sum_{j=0}^{\infty} \pi_{ij} \leq 1$ and $\pi_{ij} = \sum_{k=0}^{\infty} \pi_{ik} p_{kj} = \sum_{k=0}^{\infty} p_{ik} \pi_{kj}$. Here $p_{ij}^{(\nu)}$ is the transition probability from state i to state j in ν steps and $p_{ij} = p_{ij}^{(1)}$. For our one-step Markov chain, we have $p_{i,i-1} = \frac{\beta i^2}{4i + \beta i^2}$ and $p_{i,i+1} = \frac{4i}{4i + \beta i^2}$ as the only nonzero transition probabilities. Thus

$$p_{i,i-1} \pi_{i-1,0} + p_{i,i+1} \pi_{i+1,0} = \pi_{i0}$$

for $i \geq 1$ and the second order recurrence relation becomes

$$\pi_{i+1,0} - \pi_{i0} = \frac{\beta i}{4} (\pi_{i0} - \pi_{i-1,0}).$$

From this, it is easy to show that $\pi_{i+1,0} - \pi_{i0} = 0$ for all i (otherwise we have the contradiction $\pi_{i0} < 0$ for i sufficiently large). Furthermore $\pi_{00} = 1$ and $\pi_{0j} = 0$ if $j > 0$, since $i = 0$ is an absorbing barrier. Thus $\pi_{i0} = 1$ for all $i \geq 0$ and, furthermore, $\pi_{ij} = 0$ if $j > 0$.

Since $p_{i0}^{(\nu)}$ is an increasing function of ν , $\pi_{i0} = 1$ implies $\lim_{\nu \rightarrow \infty} p_{i0}^{(\nu)} = 1$. In particular, the population goes extinct along every trajectory of (9).

8 Appendix B

Here we calculate the evolution of the means and variances of the following approximation (16) to (10) about an interior equilibrium

$$\frac{\partial \Phi(x_1, x_2; t)}{\partial t} = \sum_{i=1}^2 \left(-\frac{\partial}{\partial x_i} (c_{i1} x_1 + c_{i2} x_2) \Phi + D_i \frac{\partial^2 \Phi}{\partial x_i^2} \right) \quad (19)$$

where $D_i \equiv \beta N^* n_i^*$ and $c_{ij} = \frac{\partial}{\partial n_j} (b_i - \beta N) n_i$ and these partial derivatives are evaluated at the equilibrium. That is

$$\begin{aligned} c_{11} &= \left((b_{11} - b_{12}) \frac{p_2^*}{N^*} - \beta \right) n_1^* & c_{12} &= - \left((b_{11} - b_{12}) \frac{p_1^*}{N^*} - \beta \right) n_1^* \\ c_{21} &= \left((b_{21} - b_{22}) \frac{p_2^*}{N^*} - \beta \right) n_2^* & c_{22} &= - \left((b_{21} - b_{22}) \frac{p_1^*}{N^*} + \beta \right) n_2^*. \end{aligned}$$

Using the zero boundary conditions

$$\lim_{x_1, x_2 \rightarrow \pm\infty} \Phi(x_1, x_2; t) = 0, \quad \lim_{x_1, x_2 \rightarrow \pm\infty} x_i \Phi(x_1, x_2; t) = 0, \quad \lim_{x_1, x_2 \rightarrow \pm\infty} \frac{\partial \Phi(x_1, x_2; t)}{\partial x_i} \text{ etc}$$

for $i = 1, 2$, we obtain

$$\begin{aligned} \frac{d \langle x_1^2 \rangle}{dt} &= \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x_1^2 \frac{\partial \Phi}{\partial t} dx_1 dx_2 \\ &= \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x_1^2 \left(-\frac{\partial}{\partial x_1} (c_{11} x_1 + c_{12} x_2) \Phi + D_1 \frac{\partial^2 \Phi}{\partial x_1^2} \right) dx_1 dx_2 \\ &\quad + \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x_1^2 \left(-\frac{\partial}{\partial x_2} (c_{21} x_1 + c_{22} x_2) \Phi + D_2 \frac{\partial^2 \Phi}{\partial x_2^2} \right) dx_1 dx_2 \\ &= \int_{-\infty}^{\infty} \left[x_1^2 \left(-(c_{11} x_1 + c_{12} x_2) \Phi + D_1 \frac{\partial \Phi}{\partial x_1} \right) \right] \Big|_{x_1=-\infty}^{x_1=\infty} dx_2 \\ &\quad - \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} 2x_1 \left(-(c_{11} x_1 + c_{12} x_2) \Phi + D_1 \frac{\partial \Phi}{\partial x_1} \right) dx_1 dx_2 \\ &\quad + \int_{-\infty}^{\infty} x_1^2 \left(-(c_{21} x_1 + c_{22} x_2) \Phi + D_2 \frac{\partial \Phi}{\partial x_2} \right) \Big|_{x_2=-\infty}^{x_2=\infty} dx_1 \\ &= 2c_{11} \langle x_1^2 \rangle + 2c_{12} \langle x_1 x_2 \rangle - 2D_1 \left[x_1 \Phi \Big|_{x_1=-\infty}^{x_1=\infty} - \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \Phi dx_1 dx_2 \right] \\ &= 2c_{11} \langle x_1^2 \rangle + 2c_{12} \langle x_1 x_2 \rangle + 2D_1 \end{aligned}$$

and

$$\begin{aligned}
\frac{d \langle x_1 x_2 \rangle}{dt} &= \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x_1 x_2 \frac{\partial \Phi}{\partial t} dx_1 dx_2 \\
&= \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x_1 x_2 \left(-\frac{\partial}{\partial x_1} (c_{11} x_1 + c_{12} x_2) \Phi + D_1 \frac{\partial^2 \Phi}{\partial x_1^2} \right) dx_1 dx_2 \\
&\quad + \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x_1 x_2 \left(-\frac{\partial}{\partial x_2} (c_{21} x_1 + c_{22} x_2) \Phi + D_2 \frac{\partial^2 \Phi}{\partial x_2^2} \right) dx_1 dx_2 \\
&= \int_{-\infty}^{\infty} \left[x_1 x_2 \left(-(c_{11} x_1 + c_{12} x_2) \Phi + D_1 \frac{\partial \Phi}{\partial x_1} \right) \right] \Big|_{x_1=-\infty}^{x_1=\infty} dx_2 \\
&\quad - \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x_2 \left(-(c_{11} x_1 + c_{12} x_2) \Phi + D_1 \frac{\partial \Phi}{\partial x_1} \right) dx_1 dx_2 \\
&\quad + \int_{-\infty}^{\infty} x_1 x_2 \left(-(c_{21} x_1 + c_{22} x_2) \Phi + D_2 \frac{\partial \Phi}{\partial x_2} \right) \Big|_{x_2=-\infty}^{x_2=\infty} dx_1 \\
&\quad - \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x_1 \left(-(c_{21} x_1 + c_{22} x_2) \Phi + D_2 \frac{\partial \Phi}{\partial x_2} \right) dx_1 dx_2 \\
&= c_{11} \langle x_1 x_2 \rangle + c_{12} \langle x_2^2 \rangle - D_1 \left[\int_{-\infty}^{\infty} x_2 \Phi \Big|_{x_1=-\infty}^{x_1=\infty} dx_2 \right] \\
&\quad + c_{21} \langle x_1^2 \rangle + c_{22} \langle x_1 x_2 \rangle - D_2 \left[\int_{-\infty}^{\infty} x_1 \Phi \Big|_{x_1=-\infty}^{x_1=\infty} dx_1 \right] - \\
&= c_{21} \langle x_1^2 \rangle + (c_{11} + c_{22}) \langle x_1 x_2 \rangle + c_{12} \langle x_2^2 \rangle.
\end{aligned}$$

That is

$$\frac{d}{dt} \begin{pmatrix} \langle x_1^2 \rangle \\ \langle x_1 x_2 \rangle \\ \langle x_2^2 \rangle \end{pmatrix} = \begin{pmatrix} 2c_{11} & 2c_{12} & 0 \\ c_{21} & c_{11} + c_{22} & c_{12} \\ 0 & 2c_{21} & 2c_{22} \end{pmatrix} \begin{pmatrix} \langle x_1^2 \rangle \\ \langle x_1 x_2 \rangle \\ \langle x_2^2 \rangle \end{pmatrix} + \begin{pmatrix} 2D_1 \\ 0 \\ 2D_2 \end{pmatrix}. \quad (20)$$

The determinant of $\begin{pmatrix} 2c_{11} & 2c_{12} & 0 \\ c_{21} & c_{11} + c_{22} & c_{12} \\ 0 & 2c_{21} & 2c_{22} \end{pmatrix}$ is $4(c_{11} + c_{22})(c_{11}c_{22} - c_{12}c_{21}) <$

0 at an ESS. By Cramer's Rule, we obtain the equilibrium of (18) as

$$\begin{pmatrix} \langle x_1^2 \rangle \\ \langle x_1 x_2 \rangle \\ \langle x_2^2 \rangle \end{pmatrix} = \frac{1}{(c_{11} + c_{22})(c_{11}c_{22} - c_{12}c_{21})} \begin{pmatrix} -(c_{11} + c_{22})c_{22}D_1 - c_{12}(c_{12}D_2 - c_{21}D_1) \\ c_{11}c_{12}D_2 + c_{21}c_{22}D_1 \\ -(c_{11} + c_{22})c_{11}D_2 - c_{21}(c_{21}D_1 - c_{12}D_2) \end{pmatrix}.$$

Furthermore, if $\begin{pmatrix} x \\ y \end{pmatrix}$ is an eigenvector of $\begin{pmatrix} c_{11} & c_{12} \\ c_{21} & c_{22} \end{pmatrix}$ with eigenvalue λ , then $\begin{pmatrix} x^2 \\ xy \\ y^2 \end{pmatrix}$ is an eigenvector of $\begin{pmatrix} 2c_{11} & 2c_{12} & 0 \\ c_{21} & c_{11} + c_{22} & c_{12} \\ 0 & 2c_{21} & 2c_{22} \end{pmatrix}$ with eigenvalue 2λ . The third eigenvalue is $c_{11} + c_{22} < 0$ with eigenvector $\begin{pmatrix} 2c_{12} \\ c_{11} - c_{22} \\ -2c_{21} \end{pmatrix}$. Thus, the equilibrium is stable if and only if p^* is an ESS.

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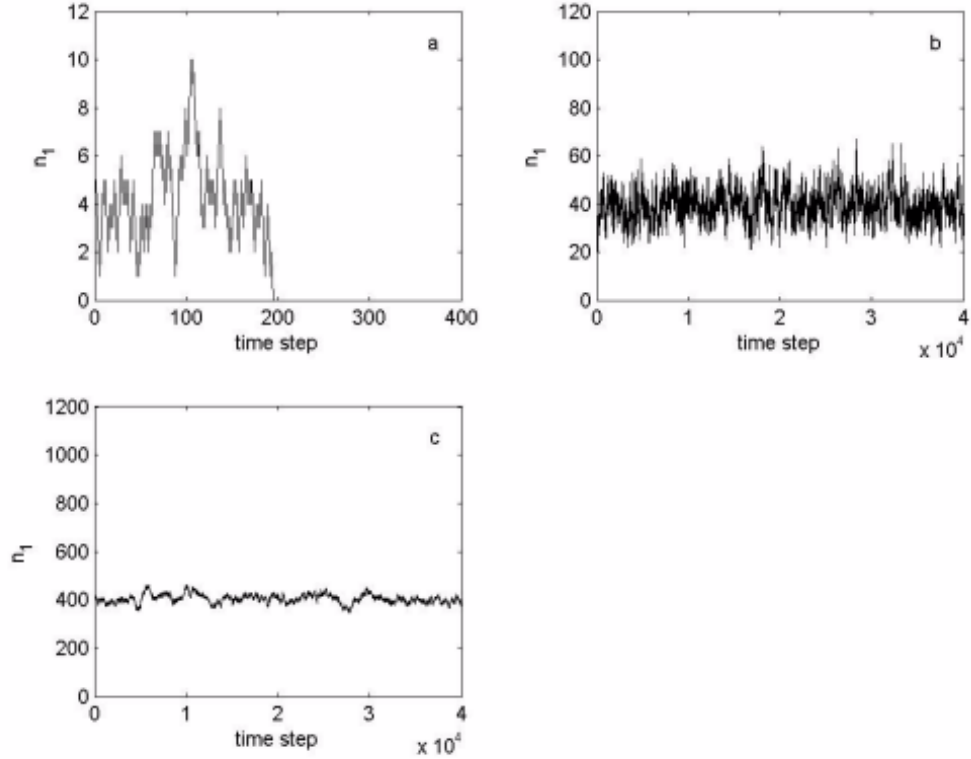


Figure 1: Sample trajectories starting at the equilibrium population size n_1^* for the discrete-time one-step process corresponding to (11) with payoff parameter $a_{11} = 3$. (a) $\beta = 1$ and $n_1^* = 4$. (b) $\beta = 0.1$ and $n_1^* = 40$. (c) $\beta = 0.01$ and $n_1^* = 400$. For this process, the transition probabilities from state i to states $i - 1$ and $i + 1$ are $p_{i,i-1} = \frac{\beta i^2}{4i + \beta i^2}$ and $p_{i,i+1} = \frac{4i}{4i + \beta i^2}$ respectively.

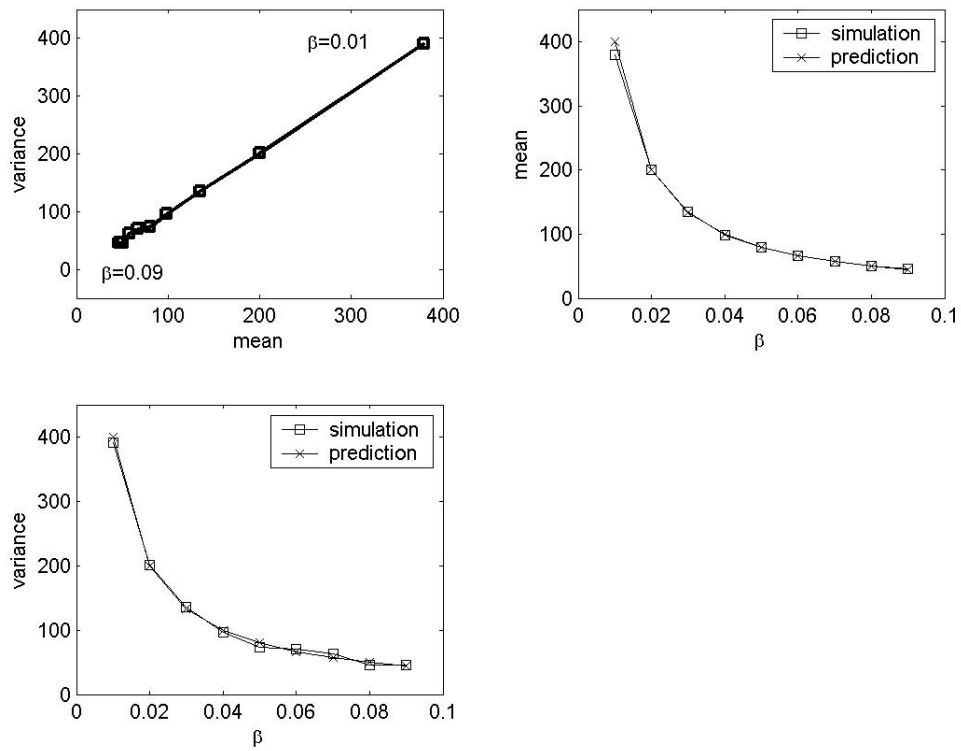


Figure 2: The means and variances of sample trajectories of (11) compared with the theoretical steady state statistics (i.e. the mean and variance) of (13). Payoff parameter is $a_{11} = 3$.

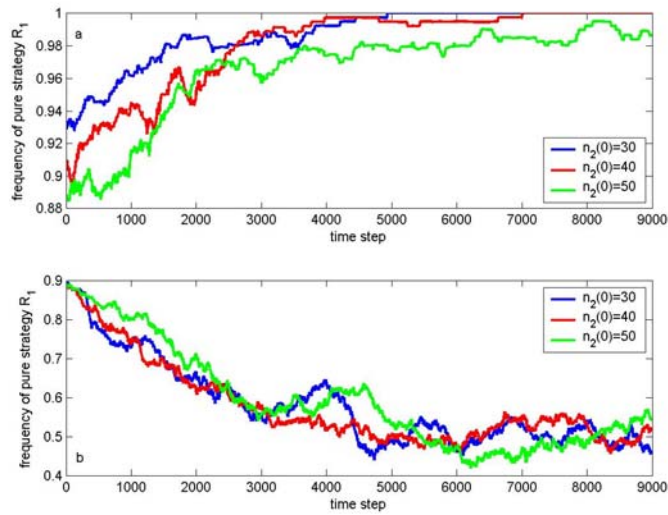


Figure 3: Stochastic simulations are plotted where most of the individuals in the population are initially R_1 -strategists. The parameter is taken as $\beta = 0.01$ and the payoff matrices are $\begin{bmatrix} 3 & 1 \\ 1 & 3 \end{bmatrix}$ and $\begin{bmatrix} 1 & 3 \\ 3 & 1 \end{bmatrix}$ in (a) and (b) respectively. The three curves in each figure correspond to three different initial conditions, which are $n_2(0) = 30, 40$ and 50 out of a total population size of 400 . The simulations in (a) show that, if most of the individuals are R_1 -strategists, the pure strategy R_2 will eventually go extinct. In (b), the population initially evolves toward the ESS proportion of fifty percent R_1 -strategists and then oscillates around this stable equilibrium.

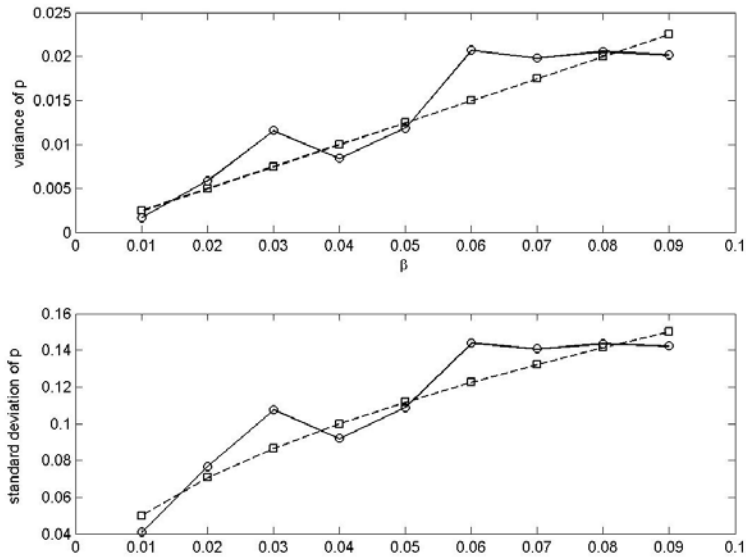


Figure 4: A comparison between Monte Carlo simulations and theoretical predictions is plotted for different values of β are taken from 0.01 to 0.09 when the payoff matrix is taken as $\begin{bmatrix} 3 & 1 \\ 1 & 3 \end{bmatrix}$. For the variance and standard deviation of phenotypic frequency p , the empty circles (connected by the solid line segments) indicate the results of the the Monte Carlo simulation, and the squares (connected by the broken curve) denote the theoretical predictions.