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Evolutionary dynamics of finite populations in games with polymorphic fitness equilibria

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Abstract

The hawk–dove (HD) game, as defined by Maynard Smith [1982. Evolution and the Theory of Games. Cambridge University Press, Cambridge], allows for a polymorphic fitness equilibrium (PFE) to exist between its two pure strategies; this polymorphism is the attractor of the standard replicator dynamics [Taylor, P.D., Jonker, L., 1978. Evolutionarily stable strategies and game dynamics. Math. Biosci. 40, 145–156; Hofbauer, J., Sigmund, K., 1998. Evolutionary Games and Population Dynamics. Cambridge University Press, Cambridge] operating on an infinite population of pure-strategists. Here, we consider stochastic replicator dynamics, operating on a finite population of pure-strategists playing games similar to HD; in particular, we examine the transient behavior of the system, before it enters an absorbing state due to sampling error. Though stochastic replication prevents the population from fixing onto the PFE, selection always favors the under-represented strategy. Thus, we may naively expect that the mean population state (of the pre-absorption transient) will correspond to the PFE. The empirical results of Fogel et al. [1997. On the instability of evolutionary stable states. BioSystems 44, 135–152] show that the mean population state, in fact, deviates from the PFE with statistical significance. We provide theoretical results that explain their observations. We show that such deviation away from the PFE occurs when the selection pressures that surround the fitness-equilibrium point are asymmetric. Further, we analyze a Markov model to prove that a finite population will generate a distribution over population states that equilibrates selection-pressure asymmetry; the mean of this distribution is generally not the fitness-equilibrium state.

Keywords: Finite population; Replicator dynamics; Selection pressure; Polymorphic fitness equilibrium; Sampling error

1. Introduction

The standard replicator dynamics (e.g., Taylor and Jonker, 1978; Hofbauer and Sigmund, 1998) are deterministic processes that operate on infinite populations. Here we examine two stochastic replicator dynamics that operate on small, well-mixed finite populations of fixed size N. These two replicator dynamics can be described as frequency-dependent Wright–Fisher (Wright, 1931; Fisher, 1930) and Moran (Moran, 1958) processes, respectively, operating on haploid populations. A population consists of pure-strategist agents; these agents play a symmetric 2×2 variable-sum game. We are particularly interested in games, such as hawk–dove (HD) (Maynard Smith, 1982), that have a polymorphic fitness equilibrium (PFE).

In the games we study, when the population state is away from the PFE, then the under-represented strategy (relative to the strategy proportions at the PFE) is always favored by selection. Thus, selection always acts to move the population state towards the PFE. Given standard replicator dynamics operating deterministically on an infinite population, this action of selection causes the PFE to be a point attractor (Hofbauer and Sigmund, 1998). Given a stochastic finite-population system, however, the role of the PFE in the system's behavior is less clear. Indeed, if our system lacks mutation, then we know that sampling error will ultimately cause the population to enter one of the two monomorphic absorbing states; but,

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the pre-absorption transient can be very long-lived—how does the PFE shape the dynamics of the population before absorption occurs? If, instead, the system includes mutation, then it will have a unique steady-state distribution over the possible population states; does the PFE correspond to the expected population state at the system's steady state?

In an empirical investigation of finite-population dynamics using agent-based computer simulation, Fogel et al. (1997) observe that the mean population state obtained under a stochastic replication process diverges from the PFE with statistical significance. We provide theoretical explication of this observation. We show that deviation away from the PFE occurs when the selection pressures that surround the PFE are asymmetric. Game payoffs determine the magnitude and shape of this asymmetry, but the amount of asymmetry to which the system is actually exposed is determined by the population's size; smaller populations are more exposed to selection-pressure asymmetry and so diverge more from the PFE.

Further, we prove with Markov-chain analysis that the finite-population process generates a distribution over population states that equilibrates asymmetries in selection pressure; the mean of the distribution is generally not the PFE. More simply put, the finite populations we study equilibrate selection pressure, not fitness.

This article is organized as follows. Section 2 reviews related work. Section 3 details the finite-population models we examine; this section specifies the class of games that we consider, discusses the calculation of the PFE, and describes the replicator dynamics that we analyze. Section 4 presents four example games that we examine in detail. Section 5 gives empirical results on these games which indicate that finite-population behavior generally does not correspond to the PFE. Section 6 proposes the hypothesis that asymmetry in selection pressure causes actual behavior to diverge from the PFE, and Section 7 formalizes this intuition. Sections 8 and 9 provide further discussion and concluding remarks. Appendix A details our agent-based simulation methods. Appendix B describes how we construct our Markov models, and Appendix C gives our central proof. Appendix D discusses the special case of very small populations in the absence of mutation. Appendix E contrasts our equation to compute fitness equilibrium in a finite population with the equation given by Schaffer (1988) to compute an evolutionarily stable strategy (ESS) in a finite population.

2. Related work

Our focus on fixed-size populations of pure-strategists and PFE stands in contrast to much other research in finite-population dynamics. For example, in their studies of ESS, Schaffer (1988), Vickery (1987, 1988), and Maynard Smith (1988) require agents to use mixed strategies. Schaffer (1988) points out that a population of N pure-strategists cannot represent an arbitrary distribution over a game's pure strategies. This is certainly true for a static population; but, when acted upon over time by a stochastic process, we can discuss the population's expected state, which can in general be an arbitrary distribution. Thus, while stochastic replication prevents the population from converging onto the PFE, we may naively suppose that the PFE will accurately describe the expected population state.

More recent work by Bergstrom and Godfrey-Smith (1998) and Orzack and Hines (2005) expands upon these earlier studies to better determine the circumstances under which a mixed strategy ESS will arise; Orzack and Hines (2005), in particular, examine a wide range of initial conditions, and consider the relationship between population size, genetic drift, and the strength of selection (we have more to say about these relationships, below). Other work on finite populations attends to issues such as invadability (Riley, 1979) and fixation probabilities of mutants (Nowak et al., 2004; Taylor et al., 2004; Lessard, 2005). Schreiber (2001) and Benaïm et al. (2004) consider the case where the population size is allowed to grow and shrink.

Most relevant to our work are the empirical investigations of Fogel et al. (1997); using agent-based computer simulation, Fogel et al. (1997) examine the dynamics of a population of 100 pure-strategists playing the HD game. In addition to using stochastic fitness-proportional replication processes, Fogel et al. (1997) consider finite-population dynamics under stochastic (and possibly incomplete) mixing and stochastic payoffs (instead of expected values). Their empirical results show that the mean population state deviates with statistical significance from the game's PFE. (Fogel and Fogel (1995) and Fogel et al. (1998), as well as other experiments in Fogel et al. (1997), use truncation-like replication processes with finite populations; see Ficici et al. (2000, 2005) for further analyses on truncation dynamics.) The work we present in this article focuses on stochastic selection and so uses (deterministic) complete mixing and expected payoffs.

Liekens et al. (2004) adopt the general methodology of our earlier work on finite populations (Ficici and Pollack, 2000) and corroborate our early results, but do so in a system that extends Ficici and Pollack (2000) to include mutation; this modification allows the system to be modeled by an irreducible Markov chain that has a unique steady-state distribution. For the present study, we begin with a zero-mutation system similar to Ficici and Pollack (2000); we model this system with a reducible Markov chain. When we arrive to our proof, we move to an irreducible Markov chain, which allows our results to generalize to the case where mutation is used.

This article expands our initial research on finite populations (Ficici and Pollack, 2000). While our original work suggests that selection-pressure asymmetry causes the observed deviation away from the PFE, it lacks the formal argument given here. Our original work limits itself to the Wright–Fisher process and assumes self-play; we now also