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The one-third law of evolutionary dynamics

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Abstract

Evolutionary game dynamics in finite populations provide a new framework for studying selection of traits with frequency-dependent fitness. Recently, a "one-third law" of evolutionary dynamics has been described, which states that strategy A fixates in a B-population with selective advantage if the fitness of A is greater than that of B when A has a frequency $\frac{1}{3}$. This relationship holds for all evolutionary processes examined so far, from the Moran process to games on graphs. However, the origin of the "number" $\frac{1}{3}$ is not understood. In this paper we provide an intuitive explanation by studying the underlying stochastic processes. We find that in one invasion attempt, an individual interacts on average with B-players twice as often as with A-players, which yields the one-third law. We also show that the one-third law implies that the average Malthusian fitness of A is positive.

Keywords: Evolutionary dynamics; Evolutionary game theory; Finite population; Fixation probability; Sojourn time

1. Introduction

Many complex traits of organisms are inherently advantageous, but provide a selective advantage only in terms of interactions between the organisms themselves. The canonical example is the trait of cooperation, whose fitness depends on the proportion of the population (or frequency) which cooperates (Nowak, 2006b). Given the importance of such interactive traits, it is of interest to understand how they evolve in a population and when they are advantageous. Evolutionary game theory provides the framework for studying the dynamics of frequency-dependent selection (Von Neumann and Morgenstern, 1944; Weibull, 1995; Hofbauer and Sigmund, 1998; Gintis, 2000; Cressman, 2003; Nowak and Sigmund, 2004; Nowak, 2006a).

Unlike in infinite populations, the game dynamics in realistic finite populations are susceptible to demographic stochasticity, hence they are described by stochastic processes rather than by deterministic equations (Maynard Smith, 1988; Schaffer, 1988; Kandori et al., 1993; Ficici and Pollack, 2000; Komarova and Nowak, 2003; Nowak et al., 2004; Taylor et al., 2004, 2006; Wild and Taylor, 2004; Imhof et al., 2005; Fudenberg et al., 2006; Nowak, 2006a; Ohtsuki and Nowak, 2006; Ohtsuki et al., 2006, 2007; Traulsen and Nowak, 2006; Traulsen et al., 2006a, 2006c, 2007a). In finite-sized populations it is possible that an advantageous mutant goes extinct. It is also possible that a deleterious mutant by chance fixates in the population. Thus, even if traits with frequency-dependent fitness seems advantageous in infinite populations, it is a priori not clear whether they can take over in finite-sized populations, and vice versa. In Nowak et al. (2004), a natural definition of an advantageous mutation was introduced, which takes into account the stochastic nature of reproduction. The fixation probability of strategy A, denoted by ρ_A, is defined as the probability that the offspring lineage of a single A-mutant invading a population of $(N-1)$ many B-individuals eventually takes over the whole population. The fixation probability of a neutral mutant is equal to the reciprocal of the population size, $1/N$. Therefore, strategy A is deemed advantageous if the fixation probability, ρ_A, is greater than $1/N$.

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If selection is weak, the likelihood of fixation ρ_A can be computed explicitly. In this case, Nowak et al. (2004) found that strategy A is advantageous if the fitness of an A-player is higher than the fitness of a B-player when the frequency of A is $\frac{1}{3}$. This has been dubbed the one-third law. We do not have, however, an intuition of why such a universal law exists, which holds for a variety of update rules and population structure studied so far. In this paper, we provide an intuition of the one-third law.

Let us consider a game with two strategies, A and B. The payoffs of A versus A, A versus B, B versus A, and B versus B, are denoted by a, b, c, and d, respectively. The payoff matrix is thus

$$\begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{array}. \tag{1}$$

The payoffs of players are dependent on the abundance of each strategy in the population. In particular, if there are i many A-players and $(N-i)$ many B-players and random pairwise interactions, then the expected payoffs of A and B are (excluding self-interaction)

$$F_i = a\frac{i-1}{N-1} + b\frac{N-i}{N-1},$$
$$G_i = c\frac{i}{N-1} + d\frac{N-i-1}{N-1}. \tag{2}$$

To account for the contribution of the game's payoff to the fitness of players, Nowak et al. (2004) introduced a "selection intensity parameter", $0 \leqslant w \leqslant 1$, such that the fitness of A and B players are, respectively, given by

$$f_i = 1 - w + wF_i,$$
$$g_i = 1 - w + wG_i. \tag{3}$$

At zero selection intensity, the game has nothing to do with one's fitness. At the other extreme, $w = 1$, fitness equals payoff. In the replicator dynamics of infinite populations, the selection intensity cancels out so that it has no effect on the evolutionary outcome. However, it is known that it crucially matters in finite populations (Traulsen et al., 2007b).

To address evolution in this approach, we now consider that reproduction and replacement occur according to some fitness-dependent rule. Nowak et al. (2004) studied the Moran process with frequency-dependent selection (details will be explained in the following sections). In the limit of weak selection, $Nw \ll 1$, they found that A is an advantageous mutant (*i.e.* $\rho_A > 1/N$) if and only if

$$(N-2)a + (2N-1)b > (N+1)c + (2N-4)d. \tag{4}$$

For large N, this condition leads to

$$a + 2b > c + 2d. \tag{5}$$

Suppose each strategy is the best reply to itself, which means $a > c$ and $b < d$. Here a single A mutant is initially at a disadvantage. The deterministic replicator equation (Taylor and Jonker, 1978; Hofbauer and Sigmund, 1998) for infinite populations tells us that a unique unstable equilibrium exists at a frequency of strategy A given by $x^* = (d-b)/[(d-b)+(a-c)]$. We can now write the one-third law of evolutionary dynamics in the form (Nowak et al., 2004)

$$x^* < \tfrac{1}{3}. \tag{6}$$

Namely, if the basin of attraction of strategy B is less than one-third then an A-mutant overcomes its initial disadvantage and fixates in the population with selective advantage (Fig. 1). Interestingly, the one-third law (6) translates the condition of advantageous mutation in finite populations into a condition on frequency-dependent fitness in infinite populations. The one-third law holds for the Moran process (Nowak et al., 2004), for the Wright–Fisher process (Lessard, 2005; Imhof and Nowak, 2006), for pairwise comparison updating (Traulsen et al., 2006b), for Cannings exchangeable models that are in the domain of application of Kingman's coalescent (Lessard and Ladret, 2007), and for games on graphs (Ohtsuki et al., 2006, 2007) with modified payoff matrices.

We study the Moran process (main text) and the Wright–Fisher process (Appendix A). We calculate the *mean effective sojourn time* at each state of the underlying stochastic process. We show that along the path of an invasion attempt, starting with a single A-mutant and ending at either extinction or fixation, an individual on average plays the game with B-players twice as often as with A-players. In other words, the number $\frac{1}{3}$ represents the proportion of A-players in all the opponents that one meets. This result leads directly to inequality (5).

This paper is structured as follows. In Section 2, we study the dynamics of fixation under neutral drift and show that the neutral mutants play with resident players on average twice as often as with other neutral mutants. In Section 3 we generalize the result for non-zero intensity of selection, leading to the one-third rule for frequency-dependent selection. We offer a discussion in Section 4.

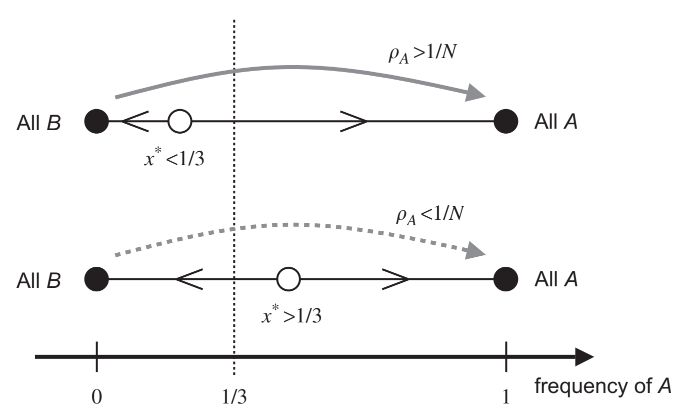

Fig. 1. The one-third law. Both A and B are Nash equilibria of the game. Top: If the location of the unstable equilibrium in the replicator equation is $x^* < \frac{1}{3}$ then the fixation probability of A is greater than $1/N$ in finite populations. Bottom: If $x^* > \frac{1}{3}$ holds, the fixation probability, ρ_A, is less than $1/N$. All these results hold for weak selection such that $Nw \ll 1$ is satisfied.