



One-third rules with equality: Second-order evolutionary stability conditions in finite populations

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ABSTRACT

The one-third law of evolutionary dynamics [Nowak et al. 2004. Emergence of cooperation and evolutionary stability in finite populations. *Nature* 428, 246–650] describes a robustness criterion for evolution in a finite population: If at an *A*-frequency of $1/3$, the fitness of an *A* player is greater (smaller) than the fitness of a *B* player, then a single *A* mutant that appears in a population of otherwise all *B* has a fixation probability greater (smaller) than the neutral threshold $1/N$, the inverse population size. We examine the case where at an *A*-frequency of $1/3$, the fitness of an *A* player is *exactly equal* to the fitness of a *B* player. We find that in this case the relative magnitude of the cross payoffs matters: If the payoff of *A* against *B* is larger (smaller) than the payoff of *B* against *A*, then a single *A* mutant has a fixation probability larger (smaller) than $1/N$. If the cross payoffs coincide, we are in the special case of a partnership game, where the deviation cost from an inefficient equilibrium is exactly balanced by the potential gain of switching to the payoff dominant equilibrium. We show that in this case the fixation probability of *A* is lower than $1/N$. Finally, we illustrate our findings by a language game with differentiated costs of signals.

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1. Introduction

Evolutionary game dynamics in a finite population follows qualitatively different laws than evolutionary dynamics in the idealized world of an infinitely large population. In a finite population the weight of each individual matters; payoff does not directly translate into offspring, but only into expected fitness. Random drift is therefore an inherent feature of such a model.

It has been remarked many times that Maynard Smith's classical notion of an *evolutionarily stable strategy* (ESS) is not suitable for a game played in a finite population (Maynard Smith, 1982, 1988; Schaffer, 1988; Nowak et al., 2004). A strategy is an ESS if it satisfies the condition that whenever only a small fraction of mutants switches to a different strategy, then, in the post-entry state of the population, the original strategy will still have a higher fitness than the mutant strategy (Maynard Smith and Price, 1973; Maynard Smith, 1982). In essence, this is the same as Hamilton's *unbeatable* strategy (Hamilton, 1967).

The formal definition of an ESS is not directly applicable to a game played in a finite population since it pre-supposes that we can consider arbitrarily small fractions of mutants. In principle, this can be overcome by looking at the smallest possible fraction

of mutants, that is, one individual who deviates to a different strategy, and then comparing the fitness of the mutant strategy to that of the resident type in the post-entry state of the population. Maynard Smith (1988) and Schaffer (1988) proposed such an approach to evolutionary stability in a finite population. But it is not clear what the dynamic foundations of this concept are in a finite population.

The central role of Maynard Smith's classical ESS concept (for infinitely large populations) derives from the fact that it translates into dynamic stability properties of particular game dynamics, most prominently, the replicator dynamics. One of the core results in evolutionary game theory is that every ESS is locally asymptotically stable in the replicator dynamics (Taylor and Jonker, 1978; Hofbauer et al., 1979; for more general accounts of evolutionary game theory see, for example, Weibull, 1995; Hofbauer and Sigmund, 1998, 2003; Cressman, 2003).

In fact, what Maynard Smith had in mind when he formulated his concept of evolutionary stability were these dynamic implications. "An ESS is a strategy", he wrote in his 1982 book, "such that if all the members of a population adopt it, then no mutant strategy could invade the population under the influences of natural selection."

However, when we consider evolutionary dynamics in a finite population, an unbeatable strategy is not necessarily protected against invasion by mutant strategies. Instead, due to the

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stochastic nature of such a process, a mutant strategy that has a lower fitness than the resident type when it first appears in the population might have some chance to reproduce and to create a lineage that finally reaches fixation throughout the whole population.

1.1. Nowak's condition

Nowak et al. (2004) propose a notion of stability for evolutionary dynamics in a finite population that takes the stochastic nature of such a process into account.

In a model of *neutral evolution*, that is, a model where drift is the only evolutionary force at work, a single mutant that appears in an otherwise monomorphic population has a chance of $1/N$, the inverse population size, to create a lineage that finally takes over to whole population. Nowak et al. (2004) compare this to a process that includes an element of selection in addition to drift. In the long run, drift induces a tendency for the fixation of a type. Nowak et al. (2004) say that *selection opposes replacement* of the resident type if the fixation probability of any mutant strategy is lower than the neutral threshold $1/N$.

More explicitly Nowak et al. (2004) consider a *frequency-dependent Moran process* for a general 2×2 symmetric game with strategies *A* and *B* and payoff matrix

$$\begin{array}{cc|cc}
 & & A & B \\
 A & a & b \\
 B & c & d
 \end{array} \quad (1)$$

Every time step one individual is chosen for reproduction proportional to its fitness, and another, randomly chosen, individual dies. The fitness of an individual, f , is composed of a fixed background fitness, and a frequency-dependent fitness component, F , the payoff of the game. Without loss of generality we can assume that the background fitness is the same for all individuals and equal to 1. Then,

$$f = (1 - \omega) + \omega F. \quad (2)$$

The parameter $\omega \in [0, 1]$ measures the intensity of selection. If $\omega = 1$, selection is strong. If $\omega = 0$, selection is not present, and we are in the case of *neutral evolution*. The condition that $\omega N \ll 1$ characterizes the case of *weak selection*; the payoff from the game is just a small component of the fitness of a type.

Eventually this process comes to an end only if the whole population is either in state “all *A*” or “all *B*”. These two population states form the absorbing boundary of the process. The probability that such a boundary state is eventually obtained, given a certain initial state, is called *fixation probability*. Specifically, let $\rho_A^{(N)}$ denote the probability that a single *A* mutant who appears in a population of otherwise all *B* creates a lineage and finally reaches fixation. If $\omega = 0$, then $\rho_A^{(N)} = 1/N$.

Nowak et al. (2004) say that strategy *B* is *evolutionarily stable in a finite population*, ESS_N , if it satisfies two conditions:

- (I) *Selection opposes A invading B*, which means that a single *A* mutant in a population of otherwise all *B* has a lower fitness than *B* (Maynard Smith's, 1988 and Schaffer's, 1988 condition); and
- (II) *selection opposes A replacing B*, which means that $\rho_A^{(N)} < 1/N$ for any $\omega > 0$.

Nowak et al. (2004) derive a *necessary* condition for ESS_N . Using a first-order approximation to assess fixation probabilities, they show that for *weak selection*, i.e., in the limit of $\omega N \searrow 0$

$$\text{if } a + 2b > c + 2d \text{ then } \rho_A^{(N)} > 1/N \text{ if } N \text{ is large enough.} \quad (3)$$

For linear fitness functions, Condition (I) requires that

$$b(N - 1) < c + d(N - 2). \quad (4)$$

Note that for large N this approaches the usual Nash condition $b < d$ (see, for example, Nowak, 2006a; for a more general discussion when Condition (I) coincides with Nash equilibrium, see Ania, 2008).

1.2. The one-third law of evolutionary dynamics

Condition (3) has inspired a number of further research projects. Interestingly it does not only hold for the frequency-dependent Moran process, but also for a variety of other processes in finite populations like the Wright–Fisher process (Lessard, 2005; Imhof and Nowak, 2006), pairwise-comparison process (Traulsen et al., 2005, 2006, 2007), and any process in the domain of Kingman's coalescent (Lessard and Ladret, 2007). Recently, it has also been shown to apply to games on graphs (Ohtsuki et al., 2006; Ohtsuki and Nowak, 2008).

Most surprisingly condition (3) translates into a criterion in terms of evolution in an infinitely large population. In the case where $c < a$ and $b < d$, and consequently “all *A*” and “all *B*” are both stable equilibria under the replicator dynamics, there is an unstable mixed equilibrium where the frequency of *A*-players is given by

$$x^* = \frac{d - b}{(d - b) + (a - c)}. \quad (5)$$

From this one can see that

$$a + 2b > c + 2d \text{ if and only if } x^* < \frac{1}{3}. \quad (6)$$

This has been called the *one-third law* of evolutionary dynamics. (See, for example, Nowak, 2006a, b. Ohtsuki et al. (2007) who develop an intuition for the one-third law. They show that along the path of an invasion attempt that starts with “all *B*”, a single individual interacts with *B* players on average twice as often as with *A* players. Hence, the number $1/3$ represents the proportion of *A* players in all the opponents with which a single player interacts on average.)

In other words, the one-third law tells us that if at an *A*-frequency of $1/3$, the fitness of an *A* player is *higher* than the fitness of a *B* player, then the fixation probability $\rho_A^{(N)}$ of a single *A* mutant in a population of otherwise all *B* exceeds $1/N$. If the fitness of *A* at frequency $1/3$ is lower than the fitness of *B*, then $\rho_A^{(N)}$ is lower than $1/N$, always provided that $\omega N \ll 1$ is large enough. But what happens if $a + 2b = c + 2d$? That is, what happens if the one-third condition holds with equality? The present paper takes up this question.

2. Mathematical analysis

We consider a general 2×2 game as given by payoff matrix (1). Let x be the number of *A* players, and $N - x$ the number of *B* players. And let F_x and G_x denote the frequency-dependent fitness component of *A* players and, respectively, *B* players:

$$\begin{aligned}
 F_x &= \frac{x-1}{N-1}a + \frac{N-x}{N-1}b \\
 G_x &= \frac{x}{N-1}c + \frac{N-x-1}{N-1}d.
 \end{aligned} \quad (7)$$

Following Eq. (2), the composed fitness functions are

$$\begin{aligned}
 f_x &= 1 + \omega(F_x - 1) \\
 g_x &= 1 + \omega(G_x - 1).
 \end{aligned} \quad (8)$$

We define, $v = \omega N$, and $p_x = (F_x - 1)/N$ and $q_x = (G_x - 1)/N$. Then

$$\begin{aligned} f_x &= 1 + vp_x, \\ g_x &= 1 + vq_x. \end{aligned} \tag{9}$$

We use $\rho_A^{(N)}(v)$ to denote the fixation probability of a single A mutant in a population of B as a function of $v = \omega N$. Then,

$$\begin{aligned} \frac{1}{\rho_A^{(N)}(v)} &= 1 + \sum_{k=1}^{N-1} \prod_{x=1}^k \frac{g_x}{f_x} \\ &= 1 + \sum_{k=1}^{N-1} \prod_{x=1}^k \frac{1 + vq_x}{1 + vp_x} = 1 + \sum_{k=1}^{N-1} \pi_k(v), \end{aligned} \tag{10}$$

where we abbreviate

$$\pi_k(v) = \prod_{x=1}^k \frac{1 + vq_x}{1 + vp_x}.$$

Note that $\pi_k(0) = 1$ for all k .

2.1. First-order conditions

To calculate $\rho_A^{(N)}(v)$ for $v \ll 1$ we consider a series expansion at $v = 0$:

$$\frac{1}{\rho_A(v)} = \frac{1}{\rho_A(0)} + \left(\frac{1}{\rho_A(0)}\right)' v + \left(\frac{1}{\rho_A(0)}\right)'' \frac{v^2}{2} + o(v^2). \tag{11}$$

We know that $\rho_A^{(N)}(0) = 1/N$. Hence, the sign of the first derivatives decides:

$$\begin{aligned} \left(\frac{1}{\rho_A^{(N)}(0)}\right)' &= \sum_{k < N} \pi_k'(0) = \sum_{k < N} (\ln \pi_k(0))' \\ &= \sum_{k < N} \sum_{x=1}^k (q_x - p_x), \end{aligned} \tag{12}$$

where we use the fact that $(\ln \pi)' = \pi'/\pi$ and $\pi_k(0) = 1$. Now, $q_x - p_x = 1/N(G_x - F_x)$. That is, the cumulated payoff differences determine the sign of the first derivative. Further,

$$G_x - F_x = \frac{c - d - a + b}{N - 1} x + \frac{a - Nb + (N - 1)d}{N - 1},$$

and

$$\begin{aligned} \sum_{x=1}^k (G_x - F_x) &= \frac{c - d - a + b(k + 1)k}{N - 1} \\ &\quad + \frac{a - Nb + (N - 1)d}{N - 1} k, \end{aligned} \tag{13}$$

whence

$$\begin{aligned} \left(\frac{1}{\rho_A^{(N)}(0)}\right)' &= \frac{6(N - 1)}{N^2} [(N + 1)c \\ &\quad + (2N - 4)d - (N - 2)a - (2N - 1)b]. \end{aligned} \tag{14}$$

Therefore, as stated in Nowak et al. (2004):

$$\begin{aligned} \text{if } (N - 2)a + (2N - 1)b > (N + 1)c + (2N - 4)d \\ \text{then } \rho_A^{(N)} > \frac{1}{N}. \end{aligned} \tag{15}$$

For large N , this leads to the condition that

$$\text{if } a + 2b > c + 2d \text{ then } \rho_A^{(N)} > \frac{1}{N}. \tag{16}$$

Likewise,

$$\text{if } a + 2b < c + 2d \text{ then } \rho_A^{(N)} < \frac{1}{N}. \tag{17}$$

However if $a + 2b = c + 2d$, we have to look at the rest of the terms in the Eq. (15): if $2a + b + c < 4d$, then $\rho_A^{(N)} > 1/N$, and if

$2a + b + c > 4d$, then $\rho_A^{(N)} < 1/N$. Note that if $a + 2b = c + 2d$ the last two inequalities reduce to $c < b$ and $c > b$, respectively. Hence we have the following proposition:

Proposition 1. In the limit of weak selection as $v = \omega N \searrow 0$ we have

- (a) $\left. \begin{aligned} &\text{if (i) } a + 2b > c + 2d \\ &\text{or if (ii) } a + 2b = c + 2d \text{ and } c < b \end{aligned} \right\} \text{ then } \rho_A^{(N)} > 1/N,$
provided N is large enough, and
- (b) $\left. \begin{aligned} &\text{if (i) } a + 2b < c + 2d \\ &\text{or if (ii) } a + 2b = c + 2d \text{ and } c > b \end{aligned} \right\} \text{ then } \rho_A^{(N)} < 1/N,$
provided N is large enough.

If in (a) or (b) condition (ii) holds true, then this implies that $\rho_A^{(N)} > 1/N$, or respectively $\rho_A^{(N)} < 1/N$, even for all $N \geq 2$.

2.2. Second-order conditions

The only case where the first-order approximation does not allow us to assess $\rho_A^{(N)}$ relative to $1/N$ is the case where

$$a + 2b = c + 2d \text{ and } c = b. \tag{18}$$

The condition that $c = b$ characterizes the case of a so-called doubly symmetric or partnership game (see Weibull, 1995; or Hofbauer and Sigmund, 1998, and Cressman, 2003). If $c = b$, the first condition in (18) reduces to

$$a + b = 2d. \tag{19}$$

Hence, we are in the special case of a partnership game with the additional qualification that d is exactly the midpoint of a and b , so that the payoff matrix is given by

$$\begin{bmatrix} a & b \\ b & \frac{a+b}{2} \end{bmatrix}. \tag{20}$$

Note that in order to ensure condition (4), we have to assume that $b < d = (a + b)/2$ which implies $b < a$. Now we have to look at the sign of the second-order term

$$\begin{aligned} \left(\frac{1}{\rho_A^{(N)}(0)}\right)'' &= \sum_{k < N} \pi_k''(0) = \sum_{k < N} [(\log \pi_k)''(0) + (\pi_k'(0))^2] \\ &= \sum_{k < N} \left[\sum_{x=1}^k (p_x^2 - q_x^2) + \left(\sum_{y=1}^k (q_y - p_y) \right)^2 \right] \\ &= \frac{(a - b)^2}{120} N + o(N) \end{aligned} \tag{21}$$

which is positive for large N unless $a = b$. Hence $a + b = 2d$ together with $c = b \neq a$ implies $\rho_A^{(N)} < 1/N$. We are now in a position to state necessary and sufficient conditions for the comparison of $\rho_A^{(N)}$ with $1/N$ for weak selection, provided N is large.

Proposition 2. In the limit of weak selection as $v = \omega N \ll 1 \searrow 0$, if $b \neq a$:

- (a) $\rho_A^{(N)} > 1/N$ for all large N if and only if
 - (i) $a + 2b > c + 2d$ or
 - (ii) $a + 2b = c + 2d$ and $c < b$.

(b) $\rho_A^{(N)} < 1/N$ for all large N if and only if

- (i) $a + 2b < c + 2d$ or
- (ii) $a + 2b = c + 2d$ and $c \geq b$.

Note the weak inequality sign of condition (ii) in part (b). If $a = b$, then all entries in the payoff matrix (1) are the same, and we are in the case of neutral evolution, $\rho_A^{(N)} = 1/N$.

3. Applications and discussion

We consider in more detail the special case as given by payoff matrix (20). We suppose further that $b < d < a$, such that both A and B fulfill Condition (1) for an ESS_N . In traditional language, a game of this form has two (strict) Nash equilibria in pure strategies: (A, A) and (B, B) . However, the equilibrium (A, A) payoff dominates the equilibrium (B, B) . This is an example of a so-called *common interest game* (Kim and Sobel, 1995). Though games of this form seem to have an intuitive solution—in our case to coordinate on the payoff-dominant Nash equilibrium (A, A) —they pose a problem for traditional theory. Strategy B is a strict Nash strategy as well. If I expect everybody else to play B , the best I can do is also to play B . If not, I will incur a loss relative to all the other players. As a consequence—despite the fact that the payoffs of players perfectly coincide—players can be trapped in the “bad” equilibrium “all B ”.

Kim and Sobel (1995) show that if players can send costless signals in every round before playing the game, then a “language” can evolve that allows players to move out of the bad equilibrium “all B ” towards the good equilibrium “all A ”. Interestingly, language itself can reflect a strategic conflict in the form of a common interest game.

3.1. A language game

Consider a sender–receiver game in the style of Nowak and Krakauer (1999). There are n events that potentially become the object of communication, and that there are m available signs. A strategy in the role of the sender is a mapping from the set of events to the set of available signs, and a strategy in the role of the receiver is a mapping from the set of available signs to the set of events. The payoffs of the sender and the receiver coincide such that they both get a payoff of one if they correctly communicate an event, that is, if the receiver links signal s_j to event e_i in case the sender uses signal s_j if event e_i happens. Players appear in the role of the sender or in the role of the receiver with equal probabilities. A strategy for this game then, a “language”, is a pair of a strategy in the role of the sender and a strategy in the role of the receiver.

If we abstract from differences in the frequencies of events and the costs of signals, for $m = n$, any strategy that is a pair of a bijective mapping from events into signs, in the role of the sender, and the inverse of this mapping in the role of the receiver exploits the maximally available payoff (for more on optimality in sender–receiver games, see Trapa and Nowak, 2000, or Pawlowitsch, 2008; for sender–receiver games played in a finite population, see Pawlowitsch, 2007).

However, if we consider a world where events occur with different frequencies and where noise in the channel induces different costs of signals, not all of these pairs of bijective mappings will do equally well. Without any further assumptions, the language that links the event that is most frequent to the signal that is least noisy, and so on, will attain the highest available payoff for any given number of events and signals, $m = n$.

Suppose, for example, that there are two events, e_1 and e_2 , and that there are two available signs s_1 and s_2 . Event e_1 occurs with probability $3/4$ and e_2 with the complementary probability $1/4$.

Sign s_1 has a perfect channel such that its transmission probability is 1, whereas sign s_2 gets through with probability $1/5$. Let L_1 denote the language that links e_1 to s_1 and e_2 to s_2 , and let L_2 denote the language that links e_1 to s_2 and e_2 to s_1 . Then the payoff of an individual using L_1 interacting with another individual who uses L_1 is $3/4 + (1/4)(1/5) = 4/5$, whereas the payoff of L_2 interacting with L_2 is $(3/4)(1/5) + (1/4) = 2/5$. Otherwise payoffs are 0. Hence, the payoff matrix for this language game is exactly of the form of our special case,

$$\begin{matrix} & L_1 & L_2 \\ L_1 & \begin{matrix} 4/5 & 0 \end{matrix} \\ L_2 & \begin{matrix} 0 & 2/5 \end{matrix} \end{matrix} \quad (22)$$

If players were to choose their language from scratch, the efficient equilibrium strategy L_1 might prove to be sufficiently focal. But language is a case par excellence where initial conditions and previous histories of play significantly shape the way in which players choose their strategies. For instance, the inefficient equilibrium strategy L_2 might have evolved under previously different conditions of the environment. Once L_2 has been established as the common language convention in a given community, it can become self-enforcing. Concepts of evolutionary stability test the robustness of such convention against small fractions of mutants.

3.2. The gains of drift

In an infinitely large population a mutant strategy can remain in the population only if it achieves at least the same fitness as the resident type. The line of research in the tradition of Nowak et al. (2004) emphasizes the fact that under an evolutionary dynamics in a finite population—due to its inherent forces of random drift—a mutant strategy can spread even if it attains a lower fitness than the resident type when it first appears in the population. Random drift, therefore, can be seen as an evolutionary force that pulls us out of the bad equilibrium. The one-third law, then, gives us an estimate how likely this is.

Nowak et al. (2004) show that in the limit of large N and weak selection, if $a + 2b > c + 2b$ then the fixation probability $\rho_A^{(N)}$ of a single A mutant in a population of otherwise all B is higher than $1/N$, the inverse population size. If $a + 2b < c + 2b$ then $\rho_A^{(N)} < 1/N$. In this note we show what happens if $a + 2b = c + 2d$.

Using a first-order approximation, we find that in this case the relative magnitude of the cross payoffs becomes decisive: If $c < b$ —that is, if the payoff of the mutant strategy against the resident strategy is higher than the payoff of the resident strategy against the mutant—then the mutant strategy has a fixation probability higher than $1/N$. If $c > b$, then the mutant strategy has a fixation probability lower than $1/N$.

Only if $c = b$, the first-order approximation does not give us enough information to assess the mutant’s fixation probability relative to $1/N$. Together with the condition that $a + 2b = c + 2d$, $c = b$ implies that $d = (a + b)/2$.

In view of the discussion how likely it is to leave an inefficient equilibrium, this special case has an interesting interpretation. A more intuitive way of writing this case is

$$a - d = d - b. \quad (23)$$

That is, the *potential gain* that a mutant strategy has from play against itself relative to the payoff of the resident strategy from play against itself, $a - d$, is exactly balanced by the *loss* that the mutant strategy incurs when playing against the resident strategy relative to the payoff of the resident strategy from play against itself, $d - b$. Our analysis of the second-order term shows that in this case the system tends to be conservative, $\rho_A^{(N)} < 1/N$.

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