

**ON RISK-DOMINANCE AND THE ‘1/3-RULE’
IN 2×2 EVOLUTIONARY GAMES**

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Abstract: A 2-player evolutionary game defines frequency-dependent selection between two alleles in the haploid Moran model of population genetics. A simple inequality of fixation probabilities for the two singleton mutant types in the population is supposed to determine the risk dominant strategy in the game. Proof is developed that risk-dominance is subject to violation when the proportion of fitness that is determined by the expected payoff in the game accords with the diffusion theory scale for weak selection. The ‘1/3-rule’ of biological evolutionary game theory is also proven to be subject to violation in the limit of a large population size. Exact calculations of derivatives of fixation probabilities show the corresponding functional dependence on population size, selection intensity and the payoff coefficients. Maclaurin series clearly demonstrate the mathematical violation of these criteria under the conventional scale of weak selection.

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1. Introduction

1.1. Background

Risk-dominant strategy and the ‘1/3-rule’ in evolutionary dynamics have captured the imagination of theoretical biologists by their apparent formulaic elegance ([1], [2], [3], [4]; see also [5], [6], [7]) Evolutionary game theory in biology was originated via innovative reinterpretations of game-theoretical concepts developed in economics historically ([8], *cf.* [9]).

Two criteria commonly used in biological evolutionary game theory and its counterparts in theoretical socio-biology, including the evolution of social cooperation, will be investigated from first principles. The evolutionary game considered pertains to the Moran model ([10], [11], [12]) with genuine frequency-dependent selection between two alleles at a single genetic locus in a haploid population of size N . Frequency-dependent selection is the most prominent class of selection models in evolutionary game theory, which originates in population genetics and theoretical ecology (see, for example, [13]). Frequency-dependent selection in the haploid model attracts research activity with computer simulation and theoretical approximations to the observed population dynamics [14]. Random genetic drift is recognized increasingly as an important modelling feature in finite populations with exchange value socialization for evolutionary anthropology [15].

The ethos of the ‘1/3-rule’ is that the equilibrium frequency of a focal strategy is less than 1/3 when selection favours its fixation in the corresponding evolutionary game, this result can be obtained from a replicator equation. The inequality that relates the ‘1/3-rule’ to the replicator, a simple first order ordinary differential equation, is a heuristic prevalent in evolutionary game theory. The derivation of the ‘1/3-rule’ more correctly proceeds from a truncation of the fixation probability of a focal strategy expressed in terms of the equilibrium of game payoff, using only a discrete Markov chain model. The final paragraphs of this Introduction contain a mathematical definition of the ‘1/3-rule’ and the replicator equation.

In this article, the ‘1/3-rule’ is proven to be violated for a finite population and to converge away from its said value in the limit of a large population size. When the singleton fixation probability of one allele is greater than another, the fitter allele is supposed to be the risk dominant strategy in the evolutionary game. In this article, risk-dominance is shown to be a condition that is only preserved when random genetic drift is infinitesimally perturbed away from neutrality The inequality that defines risk-dominance is proven to be violated

for a finite population and non-robust as $N \rightarrow \infty$. The scale of the perturbation is definitively shown here to be the square of the standard used in the diffusion theory of population genetics for weak selection ([11]; see also [16], p. 157, eqn. (5.2), where the extra factor of two in that instance is conventional for a Fisher-Wright model with discrete generations). For a review of the origins of diffusion theory that concentrates on neutrality see [17] and references therein.

A scale of selection that is proportional to $1/N$ is usual for 'weak' selection in theoretical population genetics. Diminishing this usual scale to that of its square renders the intensity of selection essentially vanishing. That is, the inequalities that yield risk-dominance and the '1/3-rule' break down unless selection is practically non-existent. This break down is a contradiction since these concepts purportedly measure the effects of weak selection on fixation probabilities. The main result here is the mathematical derivation of these conclusions.

1.2. Theoretical Introduction

Theoretical formulation of this Introduction section now proceeds (*cf.* [18], Sections 6.2 and 7.1, [3]). The population considered here is unstructured spatially and panmictic (or randomly mating). The constant population size is N , in which the number of type A individuals is i , and of type B is $N - i$. A birth-and-death process is defined as follows. Let x_i be the probability of reaching state N when starting from state i . Then, without genetic mutation in the process absorption occurs upon fixation such that $x_0 = 0$ and $x_N = 1$. Furthermore, $x_i = \beta_i x_{i-1} + (1 - \alpha_i - \beta_i) x_i + \alpha_i x_{i+1}$; for $i = 1, 2, \dots, N - 1$; where the parameters α_i , β_i give the probability of a transition $i \rightarrow i + 1$ and $i \rightarrow i - 1$, respectively. This defines a tridiagonal stochastic matrix of a Markov chain such that $\alpha_i + \beta_i \leq 1$. Let $y_i = x_i - x_{i-1}$; for $i = 1, 2, \dots, N$. These variables may be shown to satisfy, $\sum_{i=1}^N y_i = 1$, and, after some algebra, $\frac{\beta_i}{\alpha_i} = \frac{y_{i+1}}{y_i}$. Set $\gamma_i = \beta_i/\alpha_i$ then $y_{i+1} = \gamma_i y_i$ which yields

$$y_2 = \gamma_1 y_1 = \gamma_1 x_1,$$

$$y_3 = \gamma_2 y_2 = \gamma_2 (x_2 - x_1) = \gamma_2 \gamma_1 x_1,$$

$$\vdots$$

$$y_N = \gamma_{N-1} y_{N-1} = \gamma_{N-1} \dots \gamma_1 x_1. \tag{1.1}$$

Summation of terms in (1.1), yields an expression necessary in later developments,

$$1 = \sum_{i=1}^N y_i = x_1[1 + \gamma_1 + \gamma_1\gamma_2 + \dots + \gamma_1 \dots \gamma_{N-1}]. \tag{1.2}$$

Another useful expression is

$$\begin{aligned} x_i &= y_i + x_{i-1} = \gamma_{i-1}y_{i-1} + x_{i-1} \\ &= \gamma_{i-1}\gamma_{i-2}y_{i-2} + y_{i-1} + x_{i-2} \\ &= \gamma_{i-1}\gamma_{1-2} \dots \gamma_1x_1 + \gamma_{i-2} \dots \gamma_1x_1 + x_{i-2} \\ &= \gamma_{i-1} \dots \gamma_1x_1 + \gamma_{i-2} \dots \gamma_1x_1 + \dots + \gamma_1x_1 + x_1. \end{aligned} \tag{1.3}$$

Then (1.3) in succinct form is $x_i = x_1(1 + \sum_{j=1}^{i-1} \prod_{k=1}^j \gamma_k)$ Now, with (1.2) and (1.3) a foundational result is obtained ([19], Sec. 4.7; see also [16], Sec. 2.12). Thus,

$$x_i = \frac{1 + \sum_{j=1}^{i-1} \prod_{k=1}^j \gamma_k}{1 + \sum_{j=1}^{N-1} \prod_{k=1}^j \gamma_k}. \tag{1.4}$$

Consider an evolutionary game in a finite population that is analogous to the Moran model of population genetics ([2], [20], [10], [11], [16]) The payoff matrix for the pair-wise interactions in a game between two players is

$$\begin{matrix} & A & B \\ A & \begin{pmatrix} a & b \end{pmatrix} \\ B & \begin{pmatrix} c & d \end{pmatrix} \end{matrix} \tag{1.5}$$

Thus, players of the game have an expected payoff for type *A* and type *B*, respectively, given by

$$\begin{aligned} F_i &= \frac{a(i-1) + b(N-i)}{N-1} \\ G_i &= \frac{ci + d(N-i-1)}{N-1}. \end{aligned} \tag{1.6}$$

The fitness of types *A* and *B*, respectively, are

$$\begin{aligned} f_i &= 1 - \delta + \delta F_i \\ g_i &= 1 - \delta + \delta G_i \end{aligned} \tag{1.7}$$

where $0 \leq \delta \leq 1$ measures the intensity of selection by way of the proportion of fitness determined by the game. Thus, $\delta = 0$ defines a selectively neutral game, small $\delta > 0$ a game of weak selection, and $\delta = 1$ a game based on strong

selection. This describes a Moran process of frequency-dependent selection between types A and B , where (1.7) gives the fitness values.

The probability of ‘forwards’ transition of the number of type A individuals from $i \rightarrow i + 1$ in the Moran process, is

$$p_{i,i+1} = \frac{if_i}{if_i + (N - i)g_i} \frac{N - i}{N}. \tag{1.8}$$

Similarly, the probability of ‘backwards’ transition from $i \rightarrow i - 1$, is

$$p_{i,i-1} = \frac{(N - i)g_i}{if_i + (N - i)g_i} \frac{i}{N}. \tag{1.9}$$

Thus, a null transition in the process occurs with probability $1 - p_{i,i+1} - p_{i,i-1}$. Transition jumps of more than one individual occur with probability zero. The two absorbing states of this process are $i = 0$ and $i = N$.

Let the quotient of transition probabilities be

$$\frac{p_{i,i-1}}{p_{i,i+1}} = \frac{g_i}{f_i}. \tag{1.10}$$

From (1.2), the singleton fixation probability of type A is

$$\rho_A = \frac{1}{1 + \sum_{j=1}^{N-1} \prod_{i=1}^j \frac{g_i}{f_i}}. \tag{1.11}$$

Selection favours the fixation of an invading singleton mutant type if $\rho_A > 1/N$, the neutral fixation probability, and selection opposes it if $\rho_A < 1/N$. For the connection between the fixation probability and evolutionary stable strategy in related game-theoretical models see, for example, [21]. The factor $1/N$ under neutrality is because at any particular time every individual present is equally likely to eventually become the sole ancestor of the population, which is due to the random genetic drift of reproduction and expiration.

The relative frequency of gene type in the limit of a large population size yields a continuous variable x . The equilibrium relative frequency of the evolutionary game is heuristically derived from the continuous-time replicator equation ([22], [23], [24]; see also [5] and [18], Section 4.1). Note the overlapping (non-discrete) generations in the Moran model suggests the use of a continuous-time replicator. The game considered has two strategies and two replicators, $\dot{x}_A = x[f_A(x) - \varphi(x)]$ and $\dot{x}_B = x[f_B(x) - \varphi(x)]$, where $f_A(x) = ax + b(1 - x)$, $f_B(x) = cx + d(1 - x)$ and $\varphi(x) = xf_A(x) + (1 - x)f_B(x)$ define the marginal payoff functions for each strategy and the average payoff,

respectively. These equations determine the directions of selection such that a strategy with a positive difference from the population average fitness will increase as time evolves and a negative difference yields a decrease. The system of these two replicators is equivalent to a single replicator differential equation $\dot{x} = x(1-x)[f_A(x) - f_B(x)]$, where $x = x_A$, $(1-x) = x_B$. Now, from this single replicator the equilibrium frequency x^* in the population is obtained setting $\dot{x} = 0$ and solving for x to obtain $x^* = [d-b]/[a-b-c+d]$. Thus, the so-called ‘1/3-rule’ can be written down succinctly; when selection favours a focal strategy its equilibrium frequency in the replicator $x^* < \frac{1}{3}$. Note this inequality does not describe the *domain of attraction* of a focal strategy (i.e., the set of initial frequencies that converge to a fixed point in the evolution of the replicator equation). Game theory posits that a sufficient condition for the ‘1/3-rule’ is a non-neutral fixation probability of the focal strategy. That is, $\rho_A > \frac{1}{N} \Rightarrow x^* < \frac{1}{3}$. The value of 1/3 is obtained from the linearization of ρ_A in (1.11) when it is expressed in terms of x^* . In the next Section this linearization is shown to lack a valid calibration, which adversely affects derivation of the ‘1/3-rule’ from the equilibrium of game payoff in (1.6).

Whereas Kolmogorov (forward or backward) differential equations describe representations of a continuous-time Markov process with a discrete state space [19], the replicator equation is an altogether distinct and heuristic representation. Neither is the replicator a diffusion equation since it is constructed without recourse to a strong Markov property [25] or a term quantifying variance of the sample path. The only similarity that the replicator shares with diffusion theory is the continuous state variable $x = j/N$ in the limit of a large population size, and the replicator does not technically rescale time to be in units of N generations. In this sense, the replicator equation is in fact disconnected from the stochastic process that generates the population process of the Moran model. The transitions of types in the population evolve as a continuous-time Markov jump process (1.1). The Moran model is underpinned by a Markov chain that describes genetic random drift and frequency dependent selection on birth rates between the two allelic types, A and B ; refer to (1.8) and (1.9). The rigorous deterministic equivalent to the replicator for the Moran model requires drift and diffusion coefficients in a partial differential equation, which yields an accurate approximation to the stochastic evolution that corresponds to (1.1) ([10], [11]; see also [16], chapters 4 and 5). The ‘1/3-rule’ is a heuristic criterion that corresponds to the equilibrium frequency of the replicator equation. More specifically, the ‘1/3-rule’ is derived in two steps: first, linearize the fixation probability for a singleton type in the population; second, set the fixation probability to exceed the neutral value $1/N$ and simplify the resultant inequality in

terms of the equilibrium of game payoff. The drawbacks of this linearization are identified in the next Section.

2. The Equilibrium of Game Payoff Does not Yield a ‘1/3-Rule’

2.1. A Truncated Maclaurin Series for ρ_A yields the ‘1/3-rule’

The ‘1/3-rule’ has attracted a variety of theoretical developments ([4], [20], [26], [27], [28], [29], [30], [31] [32], [33]) All these works are in support of the ‘1/3-rule’, using various heuristic analytical approximations or simulation studies to justify their results. This may not be an exhaustive list of alternative heuristic approaches to the fixation probabilities under study. However, these works demonstrate that in the field of evolutionary game theory this criterion is widely utilized. An exact mathematical derivation is shown in this section and the next that must cast doubt on the veracity of the second-order negligibility assumption upon which this criterion is based.

Linearization of the fixation probability (1.11) in terms of the selection intensity δ is obtained with a Maclaurin series approximation to first order where

$$\rho_A \approx \rho_A(0) + \delta \left[\frac{d}{d\delta} \rho_A(\delta) \Big|_{\delta=0} \right] + \frac{\delta^2}{2} \left[\frac{d^2}{d\delta^2} \rho_A(\delta) \Big|_{\delta=0} \right]. \tag{2.1}$$

Let $h(\delta) = \sum_{j=1}^{N-1} \prod_{i=1}^j \frac{g_i}{f_i}$. Thus, $\rho_A = 1/[1 + h(\delta)]$. Differentiate with respect to δ , $\rho'_A(\delta) = -h'(\delta)/[1 + h(\delta)]^2$. The necessary derivative is

$$\begin{aligned} h'(\delta) &= \sum_{i=1}^{N-1} \frac{d}{d\delta} \exp \left\{ \sum_{j=1}^i \ln g_j - \ln f_j \right\} \\ &= \sum_{i=1}^{N-1} \left[\sum_{j=1}^i \frac{g'_j}{g_j} - \frac{f'_j}{f_j} \right] \left[\prod_{j=1}^i \frac{g_j}{f_j} \right]. \end{aligned} \tag{2.2}$$

In (2.1) to get the δ -term evaluate the derivative in (2.2) at $\delta = 0$. In that case, $f_j = g_j = 1$, for $j = 1, \dots, N-1$, and $h(0) = N - 1$.

These simplifications and calculation of the derivatives on the right side of (2.2) then yield

$$\begin{aligned} h'(0) &= \sum_{i=1}^{N-1} \sum_{j=1}^i G_j - F_j \\ &= \frac{1}{N-1} \sum_{i=1}^{N-1} \sum_{j=1}^i [cj + d(N-j-1) - a(j-1) - b(N-j)] \end{aligned}$$

$$\begin{aligned}
 &= \frac{1}{N-1} \sum_{i=1}^{N-1} \left[\frac{c}{2} i(i+1) + \frac{d}{2} (2(N-1)i - i(i+1)) - \frac{a}{2} i(i-1) \right. \\
 &\quad \left. - \frac{b}{2} (2Ni - i(i+1)) \right] \\
 &= \frac{c}{6} N(N+1) + \frac{d}{3} N(N-2) - \frac{a}{6} N(N-2) - \frac{b}{3} N(N - \frac{1}{2}). \tag{2.3}
 \end{aligned}$$

Evaluate the sums of index powers to get the final expression in (2.3) with elementary techniques of discrete mathematics, see for example [34]

Thus,

$$\begin{aligned}
 &\frac{d}{d\delta} \rho_A |_{\delta=0} \\
 &= \left[\frac{a}{6} \left(1 - \frac{2}{N} \right) + \frac{b}{6} \left(2 - \frac{1}{N} \right) - \frac{c}{6} \left(1 + \frac{1}{N} \right) - \frac{d}{6} \left(2 - \frac{4}{N} \right) \right]. \tag{2.4}
 \end{aligned}$$

Now consider $\rho_A > 1/N$, neglecting the second order term of the Maclaurin series (2.1) thus yields an inequality that defines the ‘1/3-rule’. That is, let $N \rightarrow \infty$ (2.4) simplifies, and is positive when

$$0 < a + 2b - c - 2d = a - b - c + d + 3(b - d). \tag{2.5}$$

Therefore, from (2.5) uncalibrated truncation yields the so-called ‘1/3-rule’ after a little algebra, obtained by equating $F_i = G_i$ from (1.6) for the evolutionary game’s equilibrium frequency in the limit of a large population size. Crucially, the validity of (2.5) is dependent on the negligibility of the second order term in (2.1).

2.2. Strict Convergence to the ‘1/3-Rule’ Requires Extremely Weak Selection, $\sim N^{-2}$

The second order term in (2.1) depends on calculation of the next derivative,

$$\frac{d^2}{d\delta^2} \rho_A(\delta) = \frac{-h''(\delta) [1 + h(\delta)] + 2 [h'(\delta)]^2}{[1 + h(\delta)]^3}. \tag{2.6}$$

Differentiate $h'(\delta)$ again

$$h''(\delta) =$$

$$\sum_{i=1}^{N-1} \left[\prod_{j=1}^i \frac{g_j}{f_j} \right] \left(\left[\sum_{j=1}^i \left(\frac{f'_j}{f_j} \right)^2 - \left(\frac{g'_j}{g_j} \right)^2 \right] + \left[\sum_{j=1}^i \frac{g'_j}{g_j} - \frac{f'_j}{f_j} \right]^2 \right). \tag{2.7}$$

In (2.1) to get the δ^2 -term evaluate the derivative in (2.6) at $\delta = 0$. Then from (2.7),

$$h''(0) = \sum_{i=1}^{N-1} \left(\left[\sum_{j=1}^i 2G_j - 2F_j + F_j^2 - G_j^2 \right] + \left[\sum_{j=1}^i G_j - F_j \right]^2 \right). \tag{2.8}$$

Proceed in (2.8) with the corresponding index summation expansions similarly as were needed to obtain (2.3). Then the summation terms in (2.8), despite the unwieldy nature of the resultant fourth degree polynomial in i , dominate with terms of leading order $\mathcal{O}(N^3)$. To evaluate this polynomial in i , sums of descending factorials are useful. Namely,

$$\sum_{i=1}^{N-1} i^3 = \sum_{i=1}^{N-1} i_{(3)} + 3i_{(2)} + i_{(1)} = \frac{1}{4}N_{(4)} + N_{(3)} + \frac{1}{2}N_{(2)}$$

and

$$\sum_{i=1}^{N-1} i^4 = \sum_{i=1}^{N-1} i_{(4)} + 6i_{(3)} + 7i_{(2)} + i_{(1)} = \frac{1}{5}N_{(5)} + \frac{3}{2}N_{(4)} + \frac{7}{3}N_{(3)} + \frac{1}{2}N_{(2)},$$

where $n_{(m)} = n(n-1)\dots(n-m+1)$.

To illustrate the leading order of coefficients, the coefficient of a^2 in (2.8) is $N(N-2)(N+1)(3N-4)/[60(N-1)]$. There is another coefficient of a^2 obtained from (2.6) since

$$\frac{d^2}{d\delta^2} \rho_A|_{\delta=0} = \left\{ -h''(\delta) N^{-2} + 2 \left[h'(\delta) \right]^2 N^{-3} \right\} |_{\delta=0}. \tag{2.9}$$

Negate the coefficient of a^2 obtained in (2.8) and to it add $2N^{-3}[h'(0)]^2 = (N-2)^2/[18N]$. Thus, the δ^2 -term of the Maclaurin series after cancellations, when $\rho_A > \frac{1}{N}$, yields an inequality analogous to (2.5),

$$0 < \left[a \left(\frac{1}{3} - \frac{2}{3N} \right) + b \left(\frac{1}{3} - \frac{1}{6N} \right) - c \left(\frac{1}{3} + \frac{1}{3N} \right) - d \left(\frac{1}{3} - \frac{2}{3N} \right) \right] + \frac{\delta}{2} \left[a^2 \frac{N-2}{N} \left\{ \frac{N-2}{3} - \frac{(N+1)(3N-4)}{10(N-1)} \right\} + \dots \right], \tag{2.10}$$

where only the coefficient of a^2 is shown in (2.10), and a common factor of $1/2$ is omitted. By inspection of the resultant coefficients of (2.8), the other corresponding a, b, c, d pairs have the same leading order. Substituting the summation terms from (2.3) and (2.8) into (2.9) demonstrates that $\frac{d^2}{d\delta^2}\rho_A(\delta)|_{\delta=0}$ is $\mathcal{O}(N)$. Therefore, $\rho_A \approx \frac{1}{N} + \delta[\mathcal{O}(1)] + \frac{\delta^2}{2}[\mathcal{O}(N)] \Rightarrow \delta \sim N^{-2}$ preserves the ‘1/3-rule’. That is, substitute $\rho_A > 1/N$ into the second order Maclaurin series approximation of ρ_A and deduce the result after cancellations. Namely, the resultant inequality has two $\frac{1}{N}$ terms that subtract out then a factor δ cancels out from the remainder. Therefore, in the limit of a large population size under weak selection when $\delta \sim N^{-1}$, the inequality (2.10) contains extraneous terms that destroy the inequality (2.5) used to define the ‘1/3-rule’.

Technically, small values of a parameter $\sigma = \lim_{N \rightarrow \infty} \delta N$ can achieve negligibility of the second order term in (2.10). This would allow empirical fine tuning of δ based on the payoff coefficients values and the exact dependence on N . Thus, evaluation of an approximation threshold must consider exactly the dependence on N for each of the 10 unordered pairs of the four payoff coefficients a, b, c, d in the second order term of the Maclaurin series for ρ_A . Equation (2.10) demonstrates that preservation of the inequality that is used to derive the ‘1/3-rule’ requires $\delta = o(N^{-1})$. That is, $\lim_{N \rightarrow \infty} \delta N = 0$ and similarly $\lim_{N \rightarrow \infty} \delta N^2 = v$ where v is a non-negligible positive constant. This condition is ensured when reducing the magnitude of δ that corresponds to weak selection by an order of magnitude in N , in which case selection is then extremely weak. Note also the coefficient of a^2 in (2.10) tends to the value $\frac{1}{60}$ when $\delta = \frac{1}{N}$, in the limit as $N \rightarrow \infty$. For another example, when $a = 1$ and $\lim_{N \rightarrow \infty} \delta N = 10$, yield a coefficient value in that case of $\frac{1}{6} = 0.166\dots$; the inequality of the 1/3-rule is then unrecognizable.

Conditions on the parameters of the payoff matrix (1.5), a, b, c, d , can determine how the fixation probability compares to that of the neutral case, $1/N$, under these conditions [30]. However, the third line of equation (21) in [30] is incompatible with equation (2.10) for their simplified payoff matrix that puts $b = c$ and $d = (a + b)/2$, as may be verified by direct substitution, and is therefore incorrect.

3. Weak Selection Does Not Yield Risk-Dominance

Defection occurs in an encounter between two players that present opposite strategies, whereas cooperation occurs when both players present the same strategy. Risk dominance for the payoff matrix (1.5) is defined by the condi-

tion, $a + b > c + d$ ([35], [36]). Then the player of strategy A is better off under the risk of defection by its opponent in the game than is the player of strategy B. This basic idea has also been studied in a similar context with recurrent mutation in the ancestral process ([37], [38]). Risk-dominance has remained an active research topic in theoretical socio-biology: extended to multiple players with random mating [39]; on social dilemmas with rudimentary spatial population structure ([40], [41]); and with relevance to inclusive fitness and group selection [42]. A rearrangement of the quotient of singleton fixation probabilities from (1.2) and (1.4), $\rho_A = x_1, \rho_B = 1 - x_{N-1}$ yields

$$\frac{\rho_A}{\rho_B} = \prod_{i=1}^{N-1} \frac{f_i}{g_i} = \prod_{i=1}^{N-1} \frac{N - 1 - \delta(N - 1) + \delta[a(i - 1) + b(N - i)]}{N - 1 - \delta(N - 1) + \delta[ci + d(N - i - 1)]}. \quad (3.1)$$

Linearization of the quotient of singleton fixation probabilities (3.1) with a Maclaurin series requires a negligible second order term,

$$\frac{\rho_A}{\rho_B} \approx 1 + \delta \left[\frac{d}{d\delta} \frac{\rho_A}{\rho_B} \Big|_{\delta=0} \right] + \frac{\delta^2}{2} \left[\frac{d^2}{d\delta^2} \frac{\rho_A}{\rho_B} \Big|_{\delta=0} \right]. \quad (3.2)$$

Take the first two derivatives of (3.1),

$$\frac{d}{d\delta} \frac{\rho_A}{\rho_B} = \left[\prod_{i=1}^{N-1} \frac{f_i}{g_i} \right] \left[\sum_{i=1}^{N-1} \frac{f'_i}{f_i} - \frac{g'_i}{g_i} \right], \quad (3.3)$$

$$\frac{d^2}{d\delta^2} \frac{\rho_A}{\rho_B} = \left[\prod_{i=1}^{N-1} \frac{f_i}{g_i} \right] \left(\left[\sum_{i=1}^{N-1} \frac{f'_i}{f_i} - \frac{g'_i}{g_i} \right]^2 + \left[\sum_{i=1}^{N-1} \left(\frac{g'_i}{g_i} \right)^2 - \left(\frac{f'_i}{f_i} \right)^2 \right] \right). \quad (3.4)$$

Note that $f''_i = g''_i = 0$.

When $\delta = 0$, (3.3) equals $\frac{1}{2}[a(N - 2) + bN - cN - d(N - 2)]$. The condition of risk-dominance is derived from an inequality of fixation probabilities. Thus, from (3.2) and (3.3), neglect the δ^2 -term in the Maclaurin series, then $\rho_A > \rho_B$ is equivalent to $(N - 2)(a - d) > N(c - b)$. This is equation (7.21) from [18], and is often attributed to Kandori *et al.* [43] obtaining it in a similar but deterministic setting with low mutation rate. In the limit of a large population size, $a + b > c + d$. This is how the higher fixation probability is supposed to characterise the risk-dominant strategy.

When $\delta = 0$, the second derivative (3.6) is

$$\begin{aligned} & \frac{1}{4}[a(N-2) + bN - cN - d(N-2)]^2 + \sum_{i=1}^{N-1} (g'_i)^2 - (f'_i)^2 \quad (3.5) \\ &= \frac{1}{4}[a(N-2) + bN - cN - d(N-2)]^2 + [a(N-2) + bN - cN - d(N-2)] \\ & \quad - \frac{1}{N-1} \left\{ \frac{a^2}{6}(N-2)(2N-3) + \frac{ab}{3}N(N-2) + \frac{b^2}{6}N(2N-1) \right. \\ & \quad \left. - \frac{c^2}{6}N(2N-1) - \frac{cd}{3}N(N-2) - \frac{d^2}{6}(N-2)(2N-3) \right\}. \quad (3.6) \end{aligned}$$

The inequality for risk-dominance therefore fails to hold since after cancellations from the corresponding Maclaurin series (3.4), when $\rho_A > \rho_B$, (3.6) is multiplied by $\delta/(2N)$. Thus, the risk-dominance inequality is complicated by additional non-negligible terms. Clearly, the risk-dominance condition is obtained from a truncated linearization of a series that is violated unless the selection parameter $\delta \sim N^{-2}$. Such an exceedingly small perturbation away from neutrality is vanishing genetically. Note, for example, the coefficient of a^2 in (3.6) tends to the value $\frac{1}{8}$ when $\delta = \frac{1}{N}$, in the limit as $N \rightarrow \infty$.

A final remark on the higher order derivatives in the Maclaurin series. Continued differentiation of ρ_A and ρ_A/ρ_B suggests that an infinity of non-negligible terms exist to confound the corresponding inequalities. For instance, when $\delta = 0$,

$$\begin{aligned} \frac{d^3}{d\delta^3} \left(\frac{\rho_A}{\rho_B} \right) &= \left[\sum_{i=1}^{N-1} f'_i - g'_i \right]^3 \\ & \quad + 3 \left[\sum_{i=1}^{N-1} f'_i - g'_i \right] \left[\sum_{i=1}^{N-1} (g'_i)^2 - (f'_i)^2 \right] \\ & \quad + 2 \left[\sum_{i=1}^{N-1} (f'_i)^3 - (g'_i)^3 \right], \end{aligned}$$

and

$$\begin{aligned} \frac{d^4}{d\delta^4} \left(\frac{\rho_A}{\rho_B} \right) &= \left[\sum_{i=1}^{N-1} f'_i - g'_i \right]^4 \\ & \quad + 6 \left[\sum_{i=1}^{N-1} f'_i - g'_i \right]^2 \left[\sum_{i=1}^{N-1} (g'_i)^2 - (f'_i)^2 \right] \\ & \quad + 3 \left[\sum_{i=1}^{N-1} (g'_i)^2 - (f'_i)^2 \right]^2 \end{aligned}$$

$$\begin{aligned}
&+ 5\left[\sum_{i=1}^{N-1} f'_i - g'_i\right] \left[\sum_{i=1}^{N-1} (f'_i)^3 - (g'_i)^3\right] \\
&+ 6\left[\sum_{i=1}^{N-1} (g'_i)^4 - (f'_i)^4\right].
\end{aligned}$$

Therefore, coefficients of triples and double pairs, or quadruples, of a , b , c , d appear in the corresponding inequalities respectively, since $\delta^2 \frac{1}{N} \mathcal{O}(N^3)$ and $\delta^3 \frac{1}{N} \mathcal{O}(N^4)$ are not necessarily negligible under weak selection.

Note also a '1/2-rule' ([3], equation (2.58)) follows from a similar truncation to first order in a Maclaurin series of the quotient of fixation probabilities in (3.1), namely $\rho_A > \rho_B \Rightarrow x^* < \frac{1}{2}$. This rule is obtained after a slight rearrangement of the risk-dominance inequality, but still depends on the second order negligibility of the Maclaurin series which requires $\delta \sim N^{-2}$.

4. Conclusion

The results herein are primarily mathematical issues that address a variety of ideas from simulation studies and heuristic analytical developments in theoretical evolutionary socio-biology. Risk-dominance and the '1/3-rule' are mathematical inequalities commonly associated with fixation probabilities in biological evolutionary game theory. The Maclaurin series used in derivation of these criteria are proven to show non-constant convergence in the limit of a large population size under weak selection. Weak selection in population genetics is usually standardized to be on the order of the reciprocal of population size. Careful examination of the requisite derivatives upon which these two criteria depend reveals the corresponding inequalities subject to violation unless the intensity of selection is extremely weak. The inequality $\rho_A > \rho_B$ characterizes the higher fixation probability for each possible singleton mutant type in the population and is used to derive the risk-dominance condition. An evolutionary stable strategy is robust in the sense that selection resists the establishment of an alternative strategy that may arise in the population. Thus, an endemic population of strategy A is more likely to successfully resist an alternative invasive strategy B . The heuristic derivation of the '1/3-rule' relies on uncalibrated truncation of the Maclaurin series of the fixation probability for a singleton gene in the population, when this exceeds a neutral fixation probability, $\rho_A > 1/N$. Both the risk-dominance condition and the '1/3-rule' are proven non-robust, since the number of terms in the corresponding inequalities grows unless the intensity of selection $\delta \sim N^{-2}$, in the limit of a large population size. That is, the accuracy of the truncations decrease as the order of the Maclaurin series

increase. It may be of interest in future to study error thresholds of these influential criteria based on the exact dependence on finite population size, intensity of selection and payoff matrix.

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