

QUADRATIC COEFFICIENTS OF THE '1/3-RULE'
WITH FINITE POPULATION SIZE CONVERGENCE

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ABSTRACT

Frequency-dependent selection between two non-mutating strategies in a Moran model of random genetic drift yields a well-known evolutionary rule. When the fixation probability of one strategy exceeds the selectively neutral value, being the reciprocal of population size, its relative frequency in the population equilibrates to less than $1/3$. Maclaurin series of the singleton type fixation probability function calculated at second order enables the convergent domain of the payoff matrix to be obtained exactly. Results include identification of the dominant payoff matrix entries at second order with respect to potential influence on the stochastic evolution of the game. The extent of violation of this evolutionary rule can be shown to depend on the values in the payoff matrix and selection intensity. Second order coefficients obtained by direct calculus and precise algebra yield functions of population size and payoff matrix entries. The calculations herein clarify the resultant sensitivity to selection intensity when compared to previous work. Finite population size convergence quantifies the applicability of the asymptotic inequality from which the rule derives.

Keywords: Co-operation; Fixation probability; Frequency-dependent selection; Maclaurin series; Moran model.

AMS Subject Codes: 60G40; 91A22; 92D15.

1. INTRODUCTION

Fixation probabilities elementary in stochastic processes have led to advances on evolving exchange-value socialization ([11], [27], [33]). Game-theoretical models being particularly useful for studying the evolutionary dynamics of social dilemmas in groups of individuals [2]. Selection intensity between game strategies, on the order of magnitude as the reciprocal of population size, accords with the drift-diffusion partial differential equations theory of population genetics ([18]-[20]). This classic model of random genetic drift in continuous-time (with overlapping generations), akin to the discrete-time Wright-Fisher model (with intermittent generations), remains an important idealized ancestral process of modern population genetics [34]. The game-theoretical model herein does not require the assumption of a large population size, in contrast to the diffusion theory.

Consider an evolutionary game in a finite population analogous to the Moran model of population genetics ([18]-[20]). The finite population of size N consists of i players of type C (co-operators) and $N-i$ players of type D (defectors). These types do not mutate and thus represent pure strategies. The game involves pair-wise interactions being advantageous or disadvantageous between any two players according to a payoff matrix

$$\begin{array}{cc} & \begin{array}{c} C \quad D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} \alpha & \beta \\ \gamma & \delta \end{pmatrix} \end{array} \quad (1)$$

According to the first row of (1) a co-operator receives payoff α against another co-operator and receives payoff β against a defector. In the second row of (1), a defector receives payoff γ against a co-operator and receives payoff δ against another defector.

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The corresponding evolutionary game represents a *social dilemma* when $\alpha > \delta$, which ensures that exploitation of co-operators by defectors eventually yields an overall population fitness decrease as defectors approach fixation. Denote the selective parameter, $0 \leq \varpi \leq 1$, being due to the payoff differential in the game. Let the fitness of co-operation be $f_i = 1 - \varpi + \varpi F_i$, where $F_i = \frac{1}{N-1} [\alpha(i-1) + \beta(N-i)]$. Let the fitness of defection be $g_i = 1 - \varpi + \varpi G_i$, where $G_i = \frac{1}{N-1} [\gamma i + \delta(N-i-1)]$. Thus, F_i and G_i define the expected payoffs to players of type C and type D, respectively. Let $\rho_C(\varpi) = 1/[1 + h(\varpi)]$ denote the fixation probability of a singleton type C individual in the population of size N, where $h(\varpi) = \sum_{j=1}^{N-1} \prod_{i=1}^j \frac{g_i}{f_i}$. This result of stochastic processes ([9], Section 4.7) thus extends to frequency-dependent selection in the Moran model [22].

The fixation probabilities of singleton types in this model yields an evolutionary rule [21], obtained in the limit of a large population size. The second order Maclaurin series of ρ_C equals $\rho_C(\varpi) \approx \rho_C(0) + \varpi[\rho'_C(\varpi)]_{\varpi=0} + \frac{\varpi^2}{2} [\rho''_C(\varpi)]_{\varpi=0}$, where prime denotes differentiation with respect to ϖ . Derivatives must be evaluated at $\varpi = 0$, whereas convergence of the resultant second order term in the limit of a large population size requires non-zero values, $\varpi = \sigma/N$. Where σ denotes non-negative *selection intensity*. Linear truncation of the Maclaurin series yields the '1/3-rule' [21], $\rho_C(\varpi) > \frac{1}{N} \Rightarrow \frac{\delta - \beta}{\alpha - \beta - \gamma + \delta} < \frac{1}{3}$, since $[\rho'_C(\varpi)]_{\varpi=0} = \frac{\alpha}{6} \left(1 - \frac{2}{N}\right) + \frac{\beta}{6} \left(2 - \frac{1}{N}\right) - \frac{\gamma}{6} \left(1 + \frac{1}{N}\right) - \frac{\delta}{6} \left(2 - \frac{4}{N}\right)$. Note that $\rho_C(0) = \rho_D(0) = \frac{1}{N}$, the singleton type fixation probability under selective neutrality in a population of size N. This evolutionary rule, in which the population relative frequency of co-operation equilibrates to less than one-third, has attracted research on frequency-dependent selection and random genetic drift ([3], [5], [14], [15], [24], [30]). In Section 2.1, the set of second order Maclaurin series coefficients for $\rho_C(\varpi)$ will be obtained. Applicability of the '1/3-rule' remains with respect to the conundrum of evolved cooperation as an evolutionary stable strategy [23]. When defection confers advantage to the individual and cooperation confers individual disadvantage the common good or group selection must be invoked to explain altruistic behaviour, which represents an age-old problem of theoretical socio-biology [32].

This rule has endured in the literature of evolutionary game theory ([6], [31]) without analytical proof, except in one special case ([1], [25]). Computer simulation studies ([28], [29]) and early heuristic analyses ([8], [35]) had supported the validity of this rule in two-player games. Implications for the validity of the '1/3-rule' therein with generalized selection intensity are found to require modification in the Moran model, according to Theorem 1 in the present article. In theoretical socio-biology the two-player game rules are axiomatic for generalized rules in multi-player evolutionary games ([10], [12], [16]). To obtain these generalizations heuristics that simplify fixation probability truncate Maclaurin series at first order. A previous article [26] contains further details of the background theory that supplements this Introduction section. The calculations in Section 2.1, parts (i)-(x), of the present article yield a complete solution to the second order coefficients that supplant the heuristic coefficients proposed earlier [35].

2. EXTEND THE '1/3 - RULE' TO SECOND ORDER WITH MACLAURIN SERIES OF SINGLETON FIXATION PROBABILITY

The calculations in Section 2.1 parts (i) - (x) culminate in proof of Theorem 1 that describes the quadratic limiting dominant term of the inequality from which the '1/3-rule' derives. This requires the Maclaurin series of $\rho_C(\varpi)$ up to second order. Theorem 1 implicitly describes the analytical convergent domain where the '1/3-rule' remains valid.

Theorem 1: Let $\rho_C(\varpi) > \frac{1}{N}$. Then, in the limit of a large population size, the '1/3-rule' at second order yields an inequality

$$\frac{\delta - \beta}{\alpha - \beta - \gamma + \delta} < \frac{1}{3} + \frac{\sigma}{\alpha - \beta - \gamma + \delta} \left[\frac{\alpha^2}{180} + \frac{4\beta^2}{45} + \frac{\gamma^2}{180} + \frac{4\delta^2}{45} + \frac{13\alpha\beta}{180} - \frac{\alpha\gamma}{90} - \frac{13\alpha\delta}{180} - \frac{13\beta\gamma}{180} - \frac{8\beta\delta}{45} + \frac{13\gamma\delta}{180} \right] \quad (2)$$

Remarks 1:

- I. Equal payoff matrix entries, $\alpha = \beta = \gamma = \delta$, corresponds to selective neutrality. In that case, the fixation probability then equals $1/N$ the zeroth order term in the Maclaurin series. Furthermore, at finite population size N, the entire set of second order coefficients that are derived in Section 2.1 that comprise the proof of Theorem 1 sum to zero.
- II. According to inequality (2), the total value of the second order term shown being negative reduces the corresponding upper bound of the inequality such that the '1/3-rule' holds. Alternatively, the total value of the second order term shown being positive increases the corresponding upper bound of the inequality which violates the '1/3-rule'.
- III. Inequality (2) yields immediately the dominant entries of the payoff matrix (1) are β and δ , due to their product having the coefficient of largest magnitude. Comparison of both rows and both diagonals in (1) reveals symmetric influence, whereas column two $\begin{pmatrix} \cdot & \beta \\ \cdot & \delta \end{pmatrix}$ clearly dominates column one $\begin{pmatrix} \alpha & \cdot \\ \gamma & \cdot \end{pmatrix}$.

2.1 Calibration of the '1/3-rule' at second order requires ten quadratic coefficients

Proof of Theorem 1:

The second order coefficients require calculation of $[\rho_C''(\varpi)]_{\varpi=0} = [-N^{-2}h''(\varpi) + 2N^{-3}\{h'(\varpi)\}^2]_{\varpi=0}$. A special case [1] that simplifies the payoff matrix $\beta = \gamma$, $\delta = (\alpha + \beta)/2$ obtains second order coefficients in the Maclaurin series of ρ_C that equal $(\alpha - \beta)^2/120$.

The following summation ([26], equation 2.9) must be calculated to obtain the second derivative of the fixation probability

$$[h''(\varpi)]_{\varpi=0} = \sum_{i=1}^{N-1} \left[\left\{ \sum_{j=1}^i G_j - F_j \right\}^2 + \sum_{j=1}^i 2G_j - 2F_j + F_j^2 - G_j^2 \right] \tag{3}$$

After substitution of F_j and G_j , the next step calculates the entire summation of (3) that equals

$$\begin{aligned} \sum_{i=1}^{N-1} \left[(N-1)^{-2} \left\{ \sum_{j=1}^i \gamma j + \delta(N-j-1) - \alpha(j-1) - \beta(N-j) \right\}^2 \right. \\ \left. + 2(N-1)^{-1} \sum_{j=1}^i (\gamma j + \delta(N-j-1) - \alpha(j-1) - \beta(N-j)) \right. \\ \left. + (N-1)^{-2} \sum_{j=1}^i (\{\alpha(j-1) + \beta(N-j)\}^2 - \{\gamma j + \delta(N-j-1)\}^2) \right] \end{aligned} \tag{4}$$

Consider separately each of the ten quadratic coefficients that arise from the first and third inner summations of (4):

(i) Note the coefficient of α^2 herein corrects earlier work [26, equation (2.10)] that had an error of algebra. The coefficient of α^2 from $-N^{-2}h''(\varpi)$ equals

$$\begin{aligned} \frac{-1}{N^2(N-1)^2} \sum_{i=1}^{N-1} \left\{ \frac{i^2(i-1)^2}{4} + \frac{i(i-1)(2i-1)}{6} \right\} &= \frac{-1}{N^2(N-1)^2} \sum_{i=1}^{N-1} \left\{ \frac{i^4}{4} - \frac{i^3}{6} - \frac{i^2}{4} + \frac{i}{6} \right\} \\ &= \frac{-1}{N^2(N-1)^2} \left[\frac{N(N-1)(2N-1)(3N^2-3N-1)}{120} - \frac{N^2(N-1)^2}{24} - \frac{N(N-1)(2N-1)}{24} + \frac{N(N-1)}{12} \right] \\ &= \frac{-1}{N(N-1)} \left[\frac{6N^3-9N^2+N+1}{120} - \frac{N^2-N}{24} - \frac{2N-1}{24} + \frac{1}{12} \right] = \frac{-1}{N(N-1)} \left[\frac{N^3}{20} - \frac{7N^2}{60} - \frac{N}{30} + \frac{2}{15} \right] \end{aligned} \tag{5}$$

Calculation of the index powers summations in (5) and those proceeding in this Section may be obtained with sums of descending factorials ([26], p. 657; [7], equation 2.50).

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

where $i_{(m)} = i(i-1)\dots(i-m+1)$. These summations require a little algebra to get the succinct function of N for each power term shown on the middle line of (5). These formulae can also be readily verified by successive evaluation for increasing values of N . Namely, the summation of the fourth index power shown equals 1, 17, 98, 354, ...; for $N = 2, 3, 4, 5, \dots$

The part of the coefficient of α^2 from $\frac{2}{N^3}[h'(\varpi)]_{\varpi=0}^2$ equals

$$\frac{2}{N^3} \frac{1}{4} \left(\frac{N^2}{3} - \frac{2N}{3} \right)^2 = \frac{(N-2)^2}{18N} = \frac{N^3-5N^2+8N-4}{18N(N-1)} \tag{6}$$

Therefore, (5) plus (6) yields the total coefficient of α^2

$$\frac{-1}{N(N-1)} \left[N^3 \left(\frac{1}{20} - \frac{1}{18} \right) - N^2 \left(\frac{7}{60} - \frac{5}{18} \right) - N \left(\frac{1}{30} + \frac{4}{9} \right) + \frac{2}{15} + \frac{2}{9} \right] = \frac{1}{N(N-1)} \left[\frac{N^3}{180} - \frac{29N^2}{180} + \frac{43N}{90} - \frac{16}{45} \right] \tag{7}$$

Multiply (7) by $\varpi/2$ and in the limit $N \rightarrow \infty$ the dominant coefficient of α^2 equals $\frac{\sigma}{360}$;

(ii) The coefficient of β^2 from $-N^{-2}h''(\varpi)$ equals

$$\begin{aligned} \frac{-1}{N^2(N-1)^2} \sum_{i=1}^{N-1} \left\{ \frac{1}{4}i^4 - \left(N - \frac{5}{6}\right)i^3 + \left(N^2 - 2N + \frac{3}{4}\right)i^2 + \left(N^2 - N + \frac{1}{6}\right)i \right\} \\ = \frac{-1}{N(N-1)} \left[\frac{(2N-1)(3N^2-3N-1)}{120} - \left(N - \frac{5}{6}\right)\frac{N(N-1)}{4} + \left(N^2 - 2N + \frac{3}{4}\right)\frac{2N-1}{6} + \left(N^2 - N + \frac{1}{6}\right)\frac{1}{2} \right] \\ = \frac{-1}{N(N-1)} \left[\frac{2N^3}{15} + \frac{N^2}{20} - \frac{7N}{60} - \frac{1}{30} \right] \end{aligned} \tag{8}$$

The part of the coefficient of β^2 from $\frac{2}{N^3}[h'(\varpi)]_{\varpi=0}^2$ equals

$$\frac{2}{N^3} \left(\frac{N^2}{3} - \frac{N}{6} \right)^2 = \frac{(2N-1)^2}{18N} = \frac{4N^3-8N^2+5N-1}{18N(N-1)} \tag{9}$$

Therefore, (8) plus (9) yields the total coefficient of β^2

$$\frac{-1}{N(N-1)} \left[N^3 \left(\frac{2}{15} - \frac{2}{9} \right) + N^2 \left(\frac{1}{20} + \frac{4}{9} \right) - N \left(\frac{7}{60} + \frac{5}{18} \right) - \frac{1}{30} + \frac{1}{18} \right] = \frac{1}{N(N-1)} \left[\frac{4N^3}{45} - \frac{89N^2}{180} + \frac{71N}{180} - \frac{1}{45} \right] \tag{10}$$

Multiply (10) by $\varpi/2$ and in the limit $N \rightarrow \infty$ the dominant coefficient of β^2 equals $\frac{2\sigma}{45}$;

(iii) The coefficient of γ^2 from $-N^{-2}h''(\varpi)$ equals

$$\frac{-1}{N^2(N-1)^2} \sum_{i=1}^{N-1} \left\{ \frac{i^2(i+1)^2}{4} - \frac{i(i+1)(2i+1)}{6} \right\} = \frac{-1}{N^2(N-1)^2} \left[\frac{N(N-1)(2N-1)(3N^2-3N-1)}{120} + \frac{N^2(N-1)^2}{24} - \frac{N(N-1)(2N-1)}{24} - \frac{N(N-1)}{12} \right]$$

$$= \frac{-1}{N(N-1)} \left[\frac{N^3}{20} - \frac{N^2}{30} - \frac{7N}{60} - \frac{1}{30} \right] \quad (11)$$

The part of the coefficient of γ^2 from $\frac{2}{N^3}[h'(\varpi)_{\varpi=0}]^2$ equals

$$\frac{2}{N^3} \frac{1}{4} \left(\frac{N^2}{3} + \frac{N}{3} \right)^2 = \frac{(N+1)^2}{18N} = \frac{N^3+N^2-N-1}{18N(N-1)} \quad (12)$$

Therefore, (11) plus (12) yields the total coefficient of γ^2

$$\frac{-1}{N(N-1)} \left[N^3 \left(\frac{1}{20} - \frac{1}{18} \right) - N^2 \left(\frac{1}{30} + \frac{1}{18} \right) - N \left(\frac{7}{60} - \frac{1}{18} \right) - \frac{1}{30} + \frac{1}{18} \right] = \frac{1}{N(N-1)} \left[\frac{N^3}{180} + \frac{4N^2}{45} + \frac{11N}{180} - \frac{1}{45} \right]. \quad (13)$$

Multiply (13) by $\varpi/2$ and in the limit $N \rightarrow \infty$ the dominant coefficient of γ^2 equals $\frac{\sigma}{360}$;

(iv) The coefficient of δ^2 from $-N^{-2}h''(\varpi)$ equals

$$\frac{-1}{N^2(N-1)^2} \sum_{i=1}^{N-1} \left\{ \frac{1}{4}i^4 - \left(N - \frac{7}{6} \right) i^3 + \left(N^2 - 2N + \frac{3}{4} \right) i^2 - \left(N^2 - 3N + \frac{13}{6} \right) i \right\}$$

$$= \frac{-1}{N(N-1)} \left[\frac{(2N-1)(3N^2-3N-1)}{120} - \left(N - \frac{7}{6} \right) \frac{N(N-1)}{4} + \left(N^2 - 2N + \frac{3}{4} \right) \frac{2N-1}{6} - \left(N^2 - 3N + \frac{13}{6} \right) \frac{1}{2} \right]$$

$$= \frac{-1}{N(N-1)} \left[\frac{2N^3}{15} - \frac{13N^2}{15} + \frac{9N}{5} - \frac{6}{5} \right] \quad (14)$$

The part of the coefficient of δ^2 from $\frac{2}{N^3}[h'(\varpi)_{\varpi=0}]^2$ equals

$$\frac{2}{N^3} \left(\frac{N^2}{3} - \frac{2N}{3} \right)^2 = \frac{2(N-2)^2}{9N} = \frac{2(N^3-5N^2+8N-4)}{9N(N-1)} \quad (15)$$

Therefore, (14) plus (15) yields the total coefficient of δ^2

$$\frac{-1}{N(N-1)} \left[N^3 \left(\frac{2}{15} - \frac{2}{9} \right) - N^2 \left(\frac{13}{15} - \frac{10}{9} \right) + N \left(\frac{9}{5} - \frac{16}{9} \right) - \frac{6}{5} + \frac{8}{9} \right] = \frac{1}{N(N-1)} \left[\frac{4N^3}{45} - \frac{11N^2}{45} - \frac{N}{45} + \frac{14}{45} \right] \quad (16)$$

Multiply (16) by $\varpi/2$ and in the limit $N \rightarrow \infty$ the dominant coefficient of δ^2 equals $\frac{2\sigma}{45}$;

(v) The coefficient of $\alpha\beta$ from $-N^{-2}h''(\varpi)$ equals

$$\frac{-2}{N^2(N-1)^2} \sum_{i=1}^{N-1} \left\{ -\frac{i^4}{4} + (3N-2) \frac{i^3}{6} + \frac{i^2}{4} - (3N-2) \frac{i}{6} \right\}$$

$$= \frac{-2}{N(N-1)} \left[-\frac{(2N-1)(3N^2-3N-1)}{120} + \frac{(3N-2)N(N-1)}{24} + \frac{2N-1}{24} - \frac{3N-2}{12} \right] = \frac{-2}{N(N-1)} \left[\frac{3N^3}{40} - \frac{2N^2}{15} - \frac{11N}{120} + \frac{7}{60} \right] \quad (17)$$

The part of the coefficient of $\alpha\beta$ from $\frac{2}{N^3}[h'(\varpi)_{\varpi=0}]^2$ equals

$$\frac{2}{N^3} \left(\frac{N^2}{3} - \frac{2N}{3} \right) \left(\frac{N^2}{3} - \frac{N}{6} \right) = \frac{(N-2)(2N-1)}{9N} = \frac{2N^3-7N^2+7N-2}{9N(N-1)} \quad (18)$$

Therefore, (17) plus (18) yields the total coefficient of $\alpha\beta$

$$\frac{-2}{N(N-1)} \left[N^3 \left(\frac{3}{40} - \frac{1}{9} \right) - N^2 \left(\frac{2}{15} - \frac{7}{18} \right) - N \left(\frac{11}{120} + \frac{7}{18} \right) - \frac{7}{60} + \frac{1}{9} \right] = \frac{2}{N(N-1)} \left[\frac{13N^3}{360} - \frac{23N^2}{90} + \frac{173N}{360} - \frac{41}{180} \right] \quad (19)$$

Multiply (19) by $\varpi/2$ and in the limit $N \rightarrow \infty$ the dominant term coefficient of $\alpha\beta$ equals $\frac{13\sigma}{360}$;

(vi) The coefficient of $\alpha\gamma$ from $-N^{-2}h''(\varpi)$ equals

$$\frac{-2}{N^2(N-1)^2} \sum_{i=1}^{N-1} \left\{ -\frac{i(i+1)}{2} \frac{i(i-1)}{2} \right\} = \frac{1}{N(N-1)} \left[\frac{6N^3-9N^2+N+1}{60} - \frac{2N-1}{12} \right] = \frac{1}{N(N-1)} \left[\frac{N^3}{10} - \frac{3N^2}{20} - \frac{3N}{20} + \frac{1}{10} \right] \quad (20)$$

The part of the coefficient of $\alpha\gamma$ from $\frac{2}{N^3}[h'(\varpi)_{\varpi=0}]^2$ equals

$$\frac{-2}{N^3} \frac{1}{2} \left(\frac{N^2}{3} + \frac{N}{3} \right) \left(\frac{N^2}{3} - \frac{2N}{3} \right) = -\frac{(N+1)(N-2)}{9N} = \frac{-N^3+2N^2+N-2}{9N(N-1)} \quad (21)$$

Therefore, (20) plus (21) yields the total coefficient of $\alpha\gamma$

$$\frac{1}{N(N-1)} \left[N^3 \left(\frac{1}{10} - \frac{1}{9} \right) - N^2 \left(\frac{3}{20} - \frac{2}{9} \right) - N \left(\frac{3}{20} - \frac{1}{9} \right) + \frac{1}{10} - \frac{2}{9} \right] = \frac{1}{N(N-1)} \left[-\frac{N^3}{90} + \frac{13N^2}{180} - \frac{7N}{180} - \frac{11}{90} \right] \quad (22)$$

Multiply (22) by $\varpi/2$ and in the limit $N \rightarrow \infty$ the dominant coefficient of $\alpha\gamma$ equals $\frac{-\sigma}{180}$;

(vii) The coefficient of $\alpha\delta$ from $-N^{-2}h''(\varpi)$ equals

$$\frac{2}{N^2(N-1)^2} \sum_{i=1}^{N-1} \left\{ \frac{(N-1)i^2(i-1)}{2} - \frac{i^2(i^2-1)}{4} \right\} = \frac{2}{N(N-1)} \left[-\frac{(2N-1)(3N^2-3N-1)}{120} + \frac{N(N-1)^2}{8} - \frac{(2N-3)(2N-1)}{24} \right]$$

$$= \frac{2}{N(N-1)} \left[\frac{3N^3}{40} - \frac{41N^2}{120} + \frac{27N}{60} - \frac{2}{15} \right] \quad (23)$$

The part of the coefficient of $\alpha\delta$ from $\frac{2}{N^3}[h'(\varpi)_{\varpi=0}]^2$ equals

$$\frac{-2}{N^3} \left(\frac{N^2}{3} - \frac{2N}{3} \right)^2 = \frac{-2(N-2)^2}{9N} = \frac{2(-N^3+5N^2-8N+4)}{9N(N-1)} \quad (24)$$

Therefore, (23) plus (24) yields the total coefficient of $\alpha\delta$

$$\frac{2}{N(N-1)} \left[N^3 \left(\frac{3}{40} - \frac{1}{9} \right) - N^2 \left(\frac{41}{120} - \frac{5}{9} \right) + N \left(\frac{27}{60} - \frac{8}{9} \right) - \frac{2}{15} + \frac{4}{9} \right] = \frac{2}{N(N-1)} \left[-\frac{13N^3}{360} + \frac{77N^2}{360} - \frac{79N}{180} + \frac{14}{45} \right] \quad (25)$$

Multiply (25) by $\varpi/2$ and in the limit $N \rightarrow \infty$ the dominant coefficient of $\alpha\delta$ equals $\frac{-13\sigma}{360}$;

(viii) The coefficient of $\beta\gamma$ from $-N^{-2}h''(\varpi)$ equals

$$\begin{aligned} \frac{2}{N^2(N-1)^2} \sum_{i=1}^{N-1} \left\{ \frac{Ni^2(i+1)}{2} - \frac{i^2(i+1)^2}{4} \right\} &= \frac{2}{N(N-1)} \left[-\frac{(2N-1)(3N^2-3N-1)}{120} + \frac{N(N-1)^2}{8} + \frac{(2N-1)^2}{24} \right] \\ &= \frac{2}{N(N-1)} \left[\frac{3N^3}{40} - \frac{N^2}{120} - \frac{N}{20} + \frac{1}{30} \right] \end{aligned} \quad (26)$$

The part of the coefficient of $\beta\gamma$ from $\frac{2}{N^3}[h'(\varpi)_{\varpi=0}]^2$ equals

$$\frac{-2}{N^3} \left(\frac{N^2}{3} + \frac{N}{3} \right) \left(\frac{N^2}{3} - \frac{N}{6} \right) = -\frac{(N+1)(2N-1)}{9N} = \frac{-2N^3+N^2+2N-1}{9N(N-1)} \quad (27)$$

Therefore, (26) plus (27) yields the total coefficient of $\beta\gamma$

$$\frac{2}{N(N-1)} \left[N^3 \left(\frac{3}{40} - \frac{1}{9} \right) - N^2 \left(\frac{1}{120} - \frac{1}{18} \right) - N \left(\frac{1}{20} - \frac{1}{9} \right) + \frac{1}{30} - \frac{1}{18} \right] = \frac{2}{N(N-1)} \left[-\frac{13N^3}{360} + \frac{17N^2}{360} + \frac{11N}{180} - \frac{1}{45} \right] \quad (28)$$

Multiply (28) by $\varpi/2$ and in the limit $N \rightarrow \infty$ the dominant coefficient of $\beta\gamma$ equals $\frac{-13\sigma}{360}$;

(ix) The coefficient of $\beta\delta$ from $-N^{-2}h''(\varpi)$ equals

$$\begin{aligned} \frac{2}{N^2(N-1)^2} \sum_{i=1}^{N-1} \left\{ \frac{i^4}{4} - (N-1)i^3 + \left(2N^2 - 4N + \frac{3}{2} \right) \frac{i^2}{2} \right\} \\ = \frac{2}{N(N-1)} \left[\frac{(2N-1)(3N^2-3N-1)}{120} - \frac{N(N-1)^2}{4} + \frac{(2N^2-4N+\frac{3}{2})(2N-1)}{12} \right] = \frac{2}{N(N-1)} \left[\frac{2N^3}{15} - \frac{49N^2}{120} + \frac{41N}{120} - \frac{7}{60} \right] \end{aligned} \quad (29)$$

The part of the coefficient of $\beta\delta$ from $\frac{2}{N^3}[h'(\varpi)_{\varpi=0}]^2$ equals

$$\frac{-2(2)}{N^3} \left(\frac{N^2}{3} - \frac{2N}{3} \right) \left(\frac{N^2}{3} - \frac{N}{6} \right) = -\frac{2(N-2)(2N-1)}{9N} = \frac{2(-2N^3+7N^2-7N+2)}{9N(N-1)} \quad (30)$$

Therefore, (29) plus (30) yields the total coefficient of $\beta\delta$

$$\frac{2}{N(N-1)} \left[N^3 \left(\frac{2}{15} - \frac{2}{9} \right) - N^2 \left(\frac{49}{120} - \frac{7}{9} \right) + N \left(\frac{41}{120} - \frac{7}{9} \right) - \frac{7}{60} + \frac{2}{9} \right] = \frac{2}{N(N-1)} \left[-\frac{4N^3}{45} + \frac{133N^2}{360} - \frac{157N}{360} + \frac{19}{180} \right] \quad (31)$$

Multiply (31) by $\varpi/2$ and in the limit $N \rightarrow \infty$ the dominant coefficient of $\beta\delta$ equals $\frac{-4\sigma}{45}$;

(x) The coefficient of $\gamma\delta$ from $-N^{-2}h''(\varpi)$ equals

$$\begin{aligned} \frac{-2}{N^2(N-1)^2} \sum_{i=1}^{N-1} \left\{ -\frac{i^4}{4} + \left(\frac{N}{2} - \frac{2}{3} \right) i^3 + \frac{i^2}{4} - \left(\frac{N}{2} - \frac{2}{3} \right) i \right\} \\ = \frac{2}{N(N-1)} \left[\frac{(2N-1)(3N^2-3N-1)}{120} - \left(\frac{N}{2} - \frac{2}{3} \right) \frac{N(N-1)}{4} - \frac{2N-1}{24} + \left(\frac{N}{2} - \frac{2}{3} \right) \frac{1}{2} \right] = \frac{2}{N(N-1)} \left[\frac{-3N^3}{40} + \frac{13N^2}{60} + \frac{N}{120} - \frac{17}{60} \right] \end{aligned} \quad (32)$$

The part of the coefficient of $\gamma\delta$ from $\frac{2}{N^3}[h'(\varpi)_{\varpi=0}]^2$ equals

$$\frac{2}{N^3} \left(\frac{N^2}{3} + \frac{N}{3} \right) \left(\frac{N^2}{3} - \frac{2N}{3} \right) = \frac{2(N+1)(N-2)}{9N} = \frac{2(N^3-2N^2-N+2)}{9N(N-1)} \quad (33)$$

Therefore, (32) plus (33) yields the total coefficient of $\gamma\delta$

$$\frac{2}{N(N-1)} \left[N^3 \left(\frac{-3}{40} + \frac{1}{9} \right) + N^2 \left(\frac{13}{60} - \frac{2}{9} \right) + N \left(\frac{1}{120} - \frac{1}{9} \right) - \frac{17}{60} + \frac{2}{9} \right] = \frac{2}{N(N-1)} \left[\frac{13N^3}{360} - \frac{N^2}{180} - \frac{37N}{360} - \frac{11}{180} \right] \quad (34)$$

Multiply (34) by $\varpi/2$ and in the limit $N \rightarrow \infty$ the dominant coefficient of $\gamma\delta$ equals $\frac{13\sigma}{360}$.

Gather the limiting dominant terms of (7), (10), (13), (16), (19), (22), (25), (28), (31) and (34). Their sum yields the asymptotic form of the second order contribution to the '1/3-rule' inequality. The Maclaurin series at second order after cancellations of the zeroth order term, and the common factor ϖ of the first and second order terms, yields the simplified inequality

$$0 < \rho'_c(\varpi)|_{(\varpi=0)} + \frac{\varpi}{2} [\rho''_c(\varpi)|_{(\varpi=0)}] \quad (35)$$

Next, the common factor $\frac{\sigma}{60}$ of the first derivative cancels out as a divisor of the second derivative from (35) in derivation of the '1/3-rule'. Therefore, in the limit of a large population size,

$$0 < \alpha + 2\beta - \gamma - 2\delta + \frac{\sigma}{60} (\alpha^2 + 16\beta^2 + \gamma^2 + 16\delta^2 + 13\alpha\beta - 2\alpha\gamma - 13\alpha\delta - 13\beta\gamma - 32\beta\delta + 13\gamma\delta).$$

Straightforward rearrangement of that just derived to obtain the standard form of the '1/3-rule' yields Inequality (2).

This completes the proof of Theorem 1, *Q.E.D.*

2.2 Finite population size convergence

Competitive and localized sociological interactions were always a *raison d'être* of biological game theory that often models evolutionary dynamics with small population sizes ([2]). The formulae derived in parts (i)-(x) of Section 2.1 enable evaluation of population size reduction disparate with the asymptotic inequality, since the second order Maclaurin series coefficients fall short of limiting values. Models of strongly localized groups require a plausible greatest lower bound on population size such that the evolutionary rule remains meaningful; refer to Figures 1 and 2.

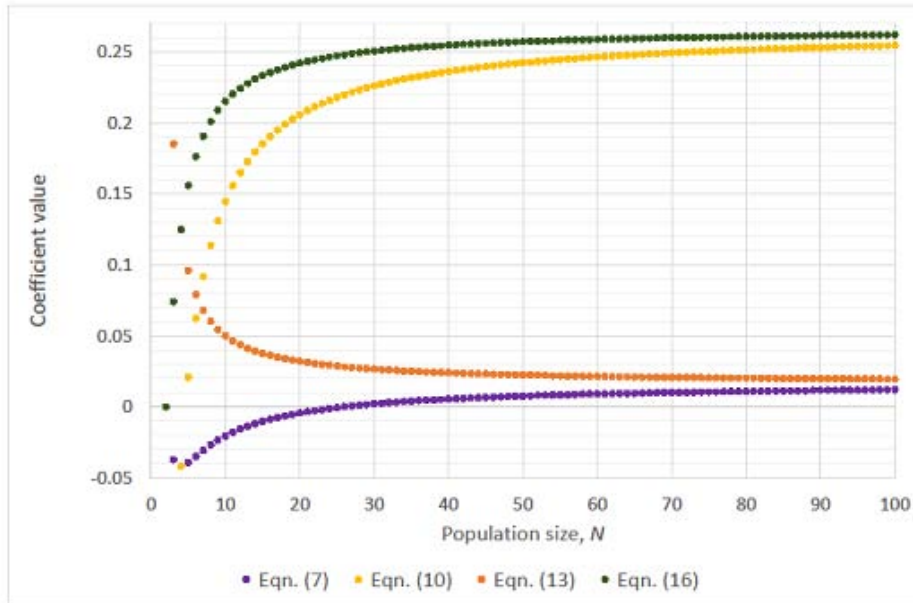


Figure-1: Formulae (7), (10), (13) and (16) when population size $N = 2, 3, \dots, 100$ yield the coefficients of α^2 , β^2 , γ^2 and δ^2 , respectively. These squared coefficients quantify negligibility of second order Maclaurin series for the singleton fixation probability. In derivation of the '1/3-rule', common factors $\frac{1}{6}$ and ϖ of the first order term are divisors of the second order term. Thus, the quantities evaluated in this plot are constituents of $3\varpi[\rho_C''(\varpi)]_{\varpi=0}$. According to Theorem 1, negligibility of the asymptotic values shown determines the validity of the '1/3-rule'. Selection intensity $\sigma = 1$.

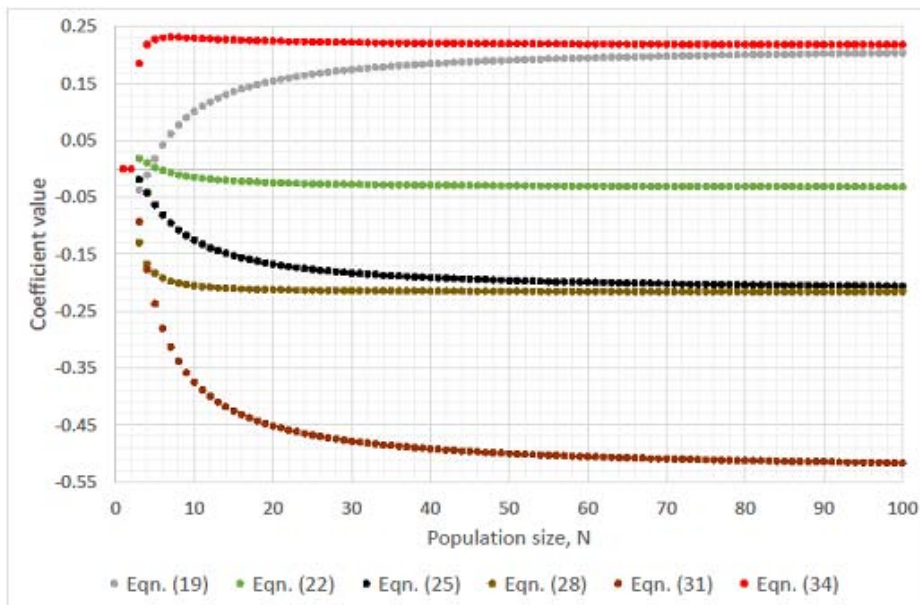


Figure-2: Formulae (19), (22), (25), (28), (31) and (34) evaluated when population size $N = 2, 3, \dots, 100$ yield the coefficients of $\alpha\beta$, $\alpha\gamma$, $\alpha\delta$, $\beta\gamma$, $\beta\delta$ (lowest curve) and $\gamma\delta$ (highest curve), respectively. These non-squared coefficients quantify negligibility of second order Maclaurin series for the singleton fixation probability. In derivation of the '1/3-rule', common factors $\frac{1}{6}$ and ϖ of the first order term are divisors of the second order term. Thus, the quantities evaluated in this plot are constituents of $3\varpi[\rho_C''(\varpi)]_{\varpi=0}$. According to Theorem 1, negligibility of the asymptotic values shown determines the validity of the '1/3-rule'. Selection intensity $\sigma = 1$.

Convergence of the '1/3-rule' quadratic coefficients can be quantified as in Figures 1 and 2, the continuation of which Table 1 summarizes.

Table-1: Convergence of the Maclaurin series second order coefficients from (35), evaluated as N increases. Set selection intensity $\sigma = 1$. Evaluation of formulae (7), (10), (16), (19), (22), (25), (28) and (31), when all multiplied by $\frac{1}{2}$, yield the corresponding coefficients of α^2 , β^2 , δ^2 , $\alpha\beta$, $\alpha\gamma$, $\alpha\delta$, $\beta\gamma$ and $\beta\delta$. The population sizes shown in the Table correspond to a minimum 90% of the asymptotic coefficient values. Note that $\alpha\gamma$, $\alpha\delta$, $\beta\gamma$ and $\beta\delta$ have negative valued coefficients. Similarly, multiplied by $\frac{1}{2}$, formula (13) of coefficient γ^2 and (34) of $\gamma\delta$ converge from above; maximum 110% of their asymptotic values at the population sizes shown.

$\tilde{N}(\alpha^2)_{-10\%}$	$\tilde{N}(\beta^2)_{-10\%}$	$\tilde{N}(\gamma^2)_{+10\%}$	$\tilde{N}(\delta^2)_{-10\%}$
278	46	172	19

$\tilde{N}(\alpha\beta)_{-10\%}$	$\tilde{N}(\alpha\gamma)_{-10\%}$	$\tilde{N}(\alpha\delta)_{-10\%}$	$\tilde{N}(\beta\gamma)_{-10\%}$	$\tilde{N}(\beta\delta)_{-10\%}$	$\tilde{N}(\gamma\delta)_{+10\%}$
60	56	48	7	31	4

The precision of Table 1 corresponds to absolute errors in small magnitude coefficients and therefore represent conservative convergence thresholds. The selection intensity being a linear scale factor the convergence behaviour of Table 1 should be robust under varied settings of σ , with the same convergence thresholds.

3. CONCLUSION

Theorem 1 restricts the '1/3-rule' such that selection intensity $\omega \sim N^{-(1+p)}$, where $0 \leq p \leq 1$. Such calibrations can be deduced that render the corresponding violations of this evolutionary rule at second order of negligible magnitude. This sharpens the calibration of the selection intensity obtained previously [26]. Quantitative analysis of error thresholds when violation of this rule occurs will clarify this qualitative statement on selection intensity.

Earlier work ([35], equation 19) proposed a dominant quadratic term of the singleton fixation probability series that resembles that obtained from (3) herein, namely $[u^2(N + 1)(N + 2) + 15uv(N + 1) + 30v^2] \frac{(N-1)(N-2)}{360}$, where $u = (a - b - c + d)/(N - 1)$ and $v = (Nb - Nd - a + d)/(N - 1)$. This almost yields an asymptotically correct leading order result with inaccuracies that diminish as finite population size N increases, except that it also inflates the result by an order of magnitude in N . Conversely, their lower order terms ([35], equation 19) remain unrecognizable by comparison with those obtained from the precise algebra in parts (i)-(x) of Section 2.1 herein. Their generalization ([35], equation 19) also includes an ill-defined heuristic multiplicative factor $[f'(0)]^2$, where $f(\beta\pi)$ is said to define any function of the product of selection intensity β and payoff π (in their notation). Whilst their appendix equation (A.4) does present the correct third order series of the singleton fixation probability that agreed with further calculus, subsequent errors of algebra and a heuristic generalized payoff function incur disagreement.

The work herein suggests a variety of further investigations on mathematical heuristics and alternative statistical processes with which this evolutionary rule arises. These include application of matrix analysis methods [8] and the Kingman coalescent of population genetics [13]. Evolutionary stability concepts in biological games often utilize drift-diffusion partial differential equations [4]. Diffusion theory approaches to the evolutionary rule considered herein have suggested robustness that extends to strong selection [36]. The '1/3-rule' observed in simulation studies where alternative statistical processes model frequency-dependent selection [17] raises further questions about the generality of this evolutionary rule.

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