CUBIC RISK-DOMINANCE INCREASES RECESSIVE CO-OPERATOR EXPLOITATION

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ABSTRACT

Frequency-dependent selection between two non-mutating strategies, co-operate or defect, with random genetic drift yields a rule of biological evolutionary game dynamics. When the quotient of singleton type fixation probability functions, that being co-operate upon defect, exceeds unity the relative frequency of the risk-dominant strategy in the population equilibrates to less than ½. Maclaurin series of this quotient of singleton type fixation probability functions calculated at second and third orders enable the convergent domain of the payoff matrix to be obtained exactly. Novel corollaries identify a reduced domain of convergence in which this evolutionary rule holds. Finite population size convergence quantifies the applicability of the asymptotic inequality from which this rule derives. Violation of this evolutionary rule depends on the normalized payoff matrix entries and selection differential. Quantitative analysis illustrates non-negligibility of the quadratic and cubic coefficients in Maclaurin series with selection being inversely proportional to population size.

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

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

1. INTRODUCTION

Evolved co-operation can persevere through various mechanisms within hawk-dove type communities where predatory individuals present a competitive strategy of antagonistic exploitation ([1], [9]). Population genetics can be utilized to explain ideal mechanisms of socio-biological evolution [24]. A key feature of such models must be to calibrate the selective differential between competing strategies ([11], [27], [23]). Herein, an idealized population where individuals present strategies of either cooperate or defect in pair-wise interactions enables characterization of the relative success of both strategies. Selection between game strategies, on the order of magnitude as the reciprocal of population size, accords with theory of 'weak' selection in population genetics [18]. A pioneering model of random genetic drift in continuous-time (with overlapping generations) ([15]-[17]) akin to the discrete-time Wright-Fisher model (with intermittent generations). Both these remain important elementary models of modern population genetics [26]. This game-theoretical model itself does not require the assumption of a large population size. Quantitative analysis herein compares finite populations to an asymptotic inequality of fixation probabilities obtained in the limit of a large population size.

Consider an evolutionary game in a finite population analogous to the haploid Moran model of population genetics ([15]-[17]). The finite population of size N consists of i players of type C (co-operators) and N-i players of type D (defectors). According to stochastic realization $i \in \{0, 1, 2, \dots, N\}$, where absorption occurs at $i = 0$ or N. These types do not mutate and thus represent pure strategies (*cf.* [14]). Population spatial structure ([10], [20]) being neglected it does not affect rates of asexual reproduction for each type. The game involves pair-wise interactions being advantageous or disadvantageous for any two players according to a payoff matrix

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

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 $\rho_C(\varpi)$ and $\rho_D(\varpi)$ denote the fixation probability of singleton type C and D individuals, respectively. An elementary result of stochastic processes yields the quotient of singleton fixation probabilities, which extends to frequency-dependent selection in the Moran model [21]; $\frac{\rho_C(\varpi)}{\rho_D(\varpi)} = \prod_{i=1}^{N-1} \frac{f_i}{g_i}$. Details of the derivation can be found elsewhere ([19], equation 3.1), including an extensive review of game-theoretical heuristics ([22], section 2.3.4).

The fixation probabilities of singleton types in this model yield an evolutionary rule [21], obtained in the limit of a large population size. The Maclaurin series for the quotient of singleton fixation probabilities yields the third order approximation $\frac{\rho_C(\varpi)}{\rho_D(\varpi)} \approx \frac{\rho_C(0)}{\rho_D(0)} + \varpi \left[\frac{\rho_C(\varpi)}{\rho_D(\varpi)}\right]' |_{(\varpi=0)} + \frac{\varpi^2}{2} \left[\frac{\rho_C(\varpi)}{\rho_D(\varpi)}\right]'' |_{(\varpi=0)} + \frac{\varpi^3}{6} \left[\frac{\rho_C(\varpi)}{\rho_D(\varpi)}\right]''' |_{(\varpi=0)}$, where prime denotes the derivatives with respect to ϖ that must be evaluated at $\varpi = 0$. Convergence of the resultant second and third order terms in the limit of a large population size requires non-zero values, $\varpi = \sigma/N$. Where σ denotes non-negative *selection intensity*. At a first order truncation of the Maclaurin series, the risk-dominance inequality states that $\rho_C(\varpi) > \rho_D(\varpi) \Rightarrow \alpha + \beta > \gamma + \delta$ ([5], [8], [21]), since $[\rho_C(\varpi)/\rho_D(\varpi)]'_{\varpi=0} = \frac{1}{2}[\alpha(N-2) + \beta N - \gamma N - \delta(N-2)]$. The risk to players being dissimilar strategy encounter; then the strategy of highest singleton fixation probability possesses the highest total payoff. Theoretical biologists have also developed this idea in social dilemmas characterizing strategic cooperation on simple networks [25].

In Section 2, second and third order Maclaurin series coefficients for the quotient of singleton fixation probabilities were obtained as Theorem 1. Thus, second order negligibility required for truncation of the Maclaurin series at first order that yields risk-dominance were obtained analytically as Corollaries 1.1 and 1.2. In Section 3.1, Figures 1 and 2, quantify finite population size convergence of these derived quadratic coefficients to their asymptotic values. In Section 3.2, qualitative precursors to non-negligible linear series truncation error are derived from payoff matrix normalization inequalities. Figure 3 quantifies violation in the rule up to its third order term extension with selection being inversely proportional to population size. The Conclusion section briefly summarizes the results and mentions some implications for future research.

2. EXTEND RISK-DOMINANCE TO THIRD ORDER WITH MACLAURIN SERIES OF THE QUOTIENT OF SINGLETON FIXATION PROBABILITY FUNCTIONS

The risk-dominance inequality can be rearranged slightly into a '*1/2-rule*' such that $\frac{\rho_C}{\rho_D} > 1$ implies

$$\alpha + \beta > \gamma + \delta$$
$$\alpha + 2\beta - \beta > \gamma + 2\delta - \delta$$
$$\alpha - \beta - \gamma + \delta > 2(\delta - \beta)$$
$$\frac{1}{2} > \frac{\delta - \beta}{\alpha - \beta - \gamma + \delta} \tag{2}$$

The calculations in Section 2.1 culminate in proof of Theorem 1 that describes the quadratic and cubic limiting dominant term of the '1/2-rule'. This requires the Maclaurin series of $\rho_C(\varpi)/\rho_D(\varpi)$ up to third order. In Sections 2.2 and 2.3, corollaries of Theorem 1 describe the convergent domain of the '1/2-rule' from non-harmful and harmful contests, respectively.

Theorem 1: *With selective non-neutrality, when $\rho_C(\varpi) > \rho_D(\varpi)$, extension of the '1/2-rule' at third order yields an inequality*

$$\frac{\delta - \beta}{\alpha - \beta - \gamma + \delta} < \frac{1}{2} + \frac{\sigma}{8(\alpha - \beta - \gamma + \delta)}[\alpha^2 + \beta^2 + \gamma^2 + \delta^2 + 2(\alpha\beta - \alpha\gamma - \alpha\delta - \beta\gamma - \beta\delta + \gamma\delta)]$$
$$+ \frac{\sigma^2}{48(\alpha - \beta - \gamma + \delta)}[\alpha^3 + \beta^3 - \gamma^3 - \delta^3 + 3(\alpha\gamma^2 + \beta\gamma^2 + \alpha\delta^2 + \beta\delta^2 + \alpha^2\beta - \gamma^2\delta)$$
$$- 3(\alpha^2\gamma + \alpha^2\delta + \beta^2\gamma + \beta^2\delta + \gamma\delta^2 - \alpha\beta^2) - 6(\alpha\beta\gamma + \alpha\beta\delta - \alpha\gamma\delta - \beta\gamma\delta)] \tag{3}$$

Remarks: *According to inequality (3), the total value of the second and third order terms shown being negative reduces the corresponding upper bound of the inequality such that the '1/2-rule' holds. Alternatively, the total value of the second and third order terms shown being positive increases the corresponding upper bound of the inequality which violates the '1/2-rule'.*

2.1 Coefficients in third order Maclaurin series for the quotient of singleton fixation probabilities

Proof of Theorem 1:

2.1.1: quadratic coefficients

Consider non-neutral fixation probabilities such that $\frac{\rho_C(\varpi)}{\rho_D(\varpi)} > 1$. Thus, the zeroth order term and the common factors ϖ and ½, cancel out of the third order Maclaurin series to yield a simplified inequality

$$0 < \alpha\left(1 - \frac{2}{N}\right) + \beta - \gamma - \delta\left(1 - \frac{2}{N}\right) + \frac{\varpi}{N}\left[\frac{\rho_C(\varpi)}{\rho_D(\varpi)}\right]'' \Big|_{(\varpi=0)} + \frac{\varpi^2}{3N}\left[\frac{\rho_C(\varpi)}{\rho_D(\varpi)}\right]''' \Big|_{(\varpi=0)} \tag{4}$$

Calculation of the second derivative, obtained in earlier work ([19], equation 3.4), yields two summation terms

$$\left(\frac{\rho_C}{\rho_D}\right)''_{(\varpi=0)} = \{\textstyle\sum_{i=1}^{N-1} F_i - G_i\}^2 + \{\textstyle\sum_{i=1}^{N-1} 2(F_i - G_i) - F_i^2 + G_i^2\}. \tag{5}$$

Equation (5) yields the quadratic coefficients of the payoff matrix entries as functions of population size. These quadratic coefficients were easily compiled from those found in earlier work ([19], equation 3.6). Calculation of the summation terms from (5) obtains the corresponding second order term in (4) that equals

$$\frac{\sigma}{N^2}\Big[\alpha^2\left(\frac{(N-2)^2}{4} - \frac{(N-2)(2N-3)}{6(N-1)}\right) + \beta^2\left(\frac{N^2}{4} - \frac{N(2N-1)}{6(N-1)}\right) + \gamma^2\left(\frac{N^2}{4} + \frac{N(2N-1)}{6(N-1)}\right) + \delta^2\left(\frac{(N-2)^2}{4} + \frac{(N-2)(2N-3)}{6(N-1)}\right)$$
$$+ 2\alpha\beta\left(\frac{N(N-2)}{4} - \frac{N(N-2)}{6(N-1)}\right) - 2\alpha\gamma\frac{N(N-2)}{4} - 2\alpha\delta\frac{(N-2)^2}{4} - 2\beta\gamma\frac{N^2}{4} - 2\beta\delta\frac{N(N-2)}{4} + 2\gamma\delta\left(\frac{N(N-2)}{4} + \frac{N(N-2)}{6(N-1)}\right)\Big] \tag{6}$$

where the common factor in (6) equals ϖ/N, after substitution of the selection intensity. Therefore, in the limit of a large population size, (6) yields the second order contribution to risk-dominance in (4),

$$0 < \alpha + \beta - \gamma - \delta + \frac{\sigma}{4}\left(\alpha^2 + \beta^2 + \gamma^2 + \delta^2 + 2(\alpha\beta - \alpha\gamma - \alpha\delta - \beta\gamma - \beta\delta + \gamma\delta)\right).$$

2.1.2: dominant cubic coefficients

Calculation of the third derivative, proceeds from that obtained in earlier work ([19], p. 660), and yields three summation terms

$$\left(\frac{\rho_C}{\rho_D}\right)'''_{(\varpi=0)} = \{\textstyle\sum_{i=1}^{N-1} F_i - G_i\}^3 + 3\{\textstyle\sum_{i=1}^{N-1} 2(F_i - G_i) - F_i^2 + G_i^2\}\{\textstyle\sum_{i=1}^{N-1} F_i - G_i\}$$
$$+ 2\{\textstyle\sum_{i=1}^{N-1} 3(G_i^2 - F_i^2) + 3(F_i - G_i) + 3(F_i^3 - G_i^3)\}. \tag{7}$$

The first summation term on the right side of (7) yields a result of $\mathcal{O}(N^3)$, the second summation term yields a product of two results each of $\mathcal{O}(N)$, and the last summation term yields a result of $\mathcal{O}(N)$. Thus, the first summation dominates, calculation of which being easily obtained from the first derivative raised to an exponent three. The resultant dominant cubic coefficients at finite population size equal $\frac{1}{8}\left(\alpha(N-2) + \beta N - \gamma N - \delta(N-2)\right)^3$. Therefore, in the limit of a large population size, (7) yields the third order contribution to risk-dominance in (4), an addition to the first and second order contributions, $0 < \alpha + \beta - \gamma - \delta + \frac{\sigma}{4}\left(\alpha^2 + \beta^2 + \gamma^2 + \delta^2 + 2(\alpha\beta - \alpha\gamma - \alpha\delta - \beta\gamma - \beta\delta + \gamma\delta)\right) + \frac{\sigma^2}{24}(\alpha^3 + \beta^3 - \gamma^3 - \delta^3 + 3(\alpha\gamma^2 + \beta\gamma^2 + \alpha\delta^2 + \beta\delta^2 + \alpha^2\beta - \gamma^2\delta) - 3(\alpha^2\gamma + \alpha^2\delta + \beta^2\gamma + \beta^2\delta + \gamma\delta^2 - \alpha\beta^2) - 6(\alpha\beta\gamma + \alpha\beta\delta - \alpha\gamma\delta - \beta\gamma\delta))$. Hence, slight rearrangement of the first order term in that just derived obtains the standard form of the '1/2-rule' and yields Inequality (3).

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

2.2 Non-harmful contests

When $\alpha < \gamma$ and $\beta < \delta$ then defectors dominate due to relatively higher payoffs. The payoff scenario $\beta < \delta$ implies non-harmful contests, or strong exploitation of co-operators by defectors. Note that $\alpha + \delta > \beta + \gamma$ ensures non-degenerate equilibria of the deterministic evolution of the game in this case.

Corollary 1.1: *Let* $\alpha = c\gamma, \beta = d\delta$, *where* $0 < c, d < 1$. *In this case, by Theorem 1 and Remarks, the '1/2-rule' fails to hold at second order when*

$$c > \frac{1}{2-d} \tag{8}$$

Proof of Corollary 1.1:

With the substitutions described the second order term of (3) equals

$$\frac{\sigma}{8[(1-d)\delta - (1-c)\gamma]}[(1-c)\gamma + (1-d)\delta]^2 \tag{9}$$

Formula (9) remains positive when $(1-d)\delta > (1-c)\gamma$. Hence, according to this condition the right side of (3) exceeds the '1/2-rule' upper bound value. Recall, the social dilemma requires $\alpha > \delta$. Now, the corresponding inequality can be rearranged, $1 > \frac{\delta}{\alpha} > \frac{1-c}{c(1-d)}$. Equivalently, $c > \frac{1-c}{1-d}$. Solve for c to obtain Inequality (8).

Corollary 1.1 being therefore proven, *Q.E.D.*

Note Corollary 1.1 implies $1 > c > \frac{1}{2}$, which constrains the exploitation of co-operators such that $\frac{1}{2}\gamma < \alpha < \gamma$.

2.3 Harmful contests

When $\alpha < \gamma$ and $\beta > \delta$ defector pairs endure combative attrition in contests. The payoff scenario $\beta > \delta$ implies harmful contests, or weak exploitation of co-operators by defectors. Note that $\alpha + \delta < \beta + \gamma$ ensures non-degenerate equilibria of the deterministic evolution of the game in this case.

Corollary 1.2: *Let $\alpha = c\gamma, \delta = b\beta$, where $0 < b, c < 1$. In this case, by Theorem 1 and Remarks, the '1/2-rule' always holds, although the upper bound value can be substantially reduced.*

Proof of Corollary 1.2:

With the substitutions described the second order term of (3) equals

$$\frac{-\sigma}{8[(1-b)\beta+(1-c)\gamma]}[(1-c)\gamma - (1-b)\beta]^2 < 0 \tag{10}$$

Hence, (10) proves the '1/2-rule' always holds with harmful contests. In this case, by (3) the upper bound value ½ can be substantially reduced as the selection intensity increases.

Corollary 1.2 being therefore proven, *Q.E.D.*

3. QUANTITATIVE VALIDITY OF THE RISK-DOMINANCE INEQUALITY

3.1 Finite population size convergence

Biological game theory [2] can model various sociological interactions with finite population sizes. Recent studies with either genetic, learned or aspirational transitions [13], the fitness value of discernment [7], and punitive actions [4] that facilitate evolved cooperative behaviour all utilize selection within small groups. The formulae derived in Section 2.1 herein enable evaluation of population size reduction disparate with the asymptotic inequality of Theorem 1, since the second order Maclaurin series coefficients exceed or 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.

Formula (6) shows the risk-dominance inequality quadratic coefficients as functions of N and their convergence can be quantified; refer to Figures 1 and 2.
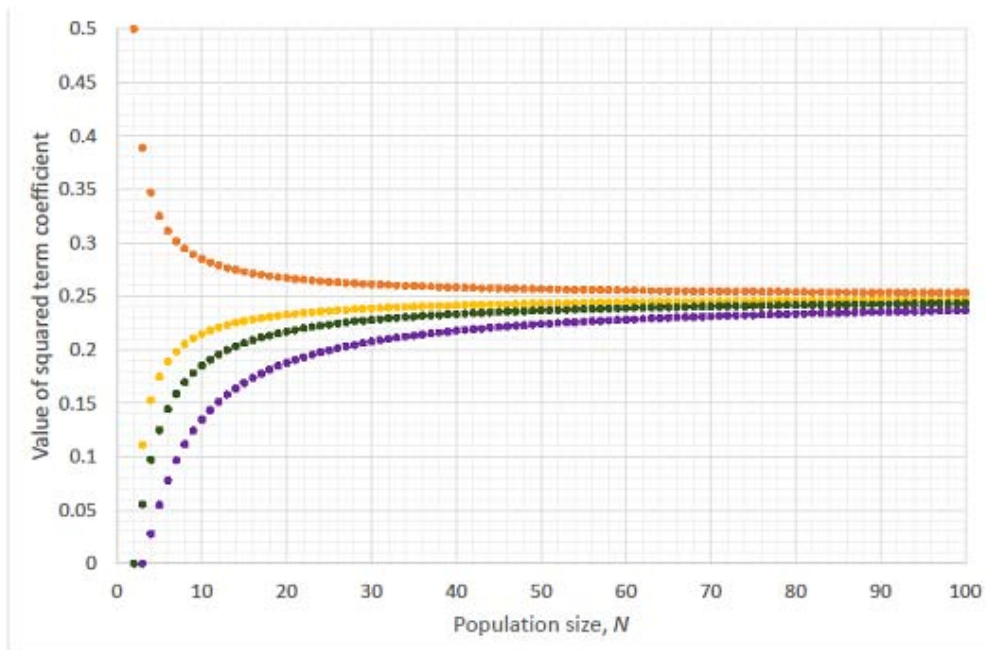

Figure-1: Formula (6) evaluated when population size $N = 2, 3, \ldots, 100$ yield the squared coefficients of α^2 (●), β^2 (●), γ^2 (●) and δ^2 (●). Selection intensity $\sigma = 1$. These squared coefficients quantify negligibility of second order Maclaurin series for the quotient of singleton fixation probabilities from (4), $\frac{\varpi}{N}\left[\left(\frac{\rho_C}{\rho_D}\right)''|_{\varpi=0}\right]$. Negligibility of the asymptotic values shown determines the validity of the risk-dominance inequality, according to Theorem 1.
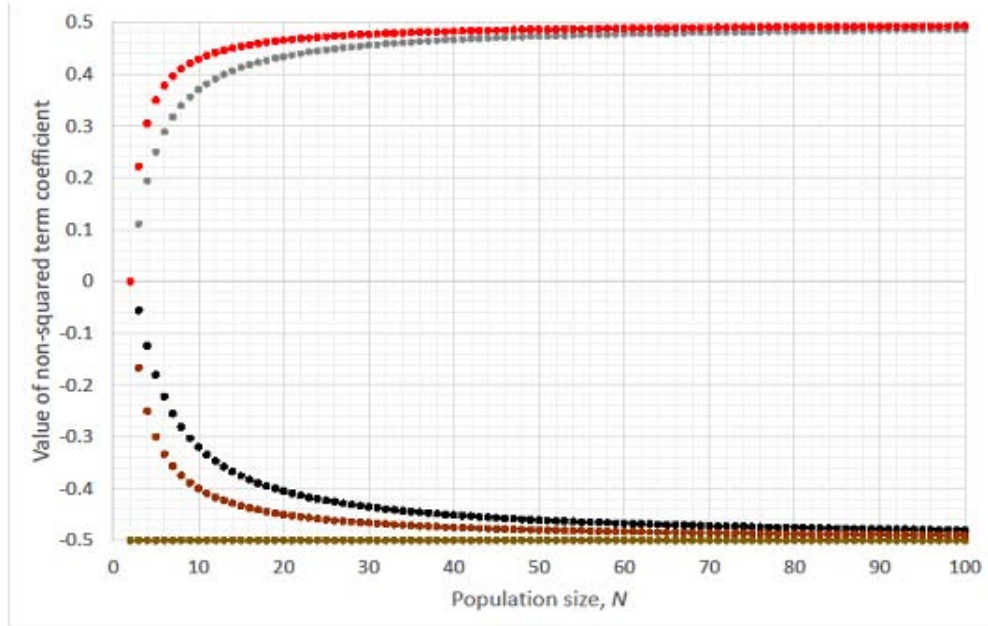
Figure-2: Formula (6) evaluated when population size $N = 2, 3, \ldots, 100$ yield non-squared quadratic coefficients of $\alpha\beta$ (●), $\alpha\delta$ (●), $\beta\delta$ (●) and $\gamma\delta$ (●). Note the coefficient of $\alpha\gamma$ equals that of $\beta\delta$ (shown), and $\beta\gamma$ (●) $\equiv -\frac{1}{2}$. Selection intensity $\sigma = 1$. These non-squared coefficients quantify negligibility of second order Maclaurin series for the quotient of singleton fixation probabilities from (4), $\frac{\varpi}{N}\left[\left(\frac{\rho_C}{\rho_D}\right)''|_{\varpi=0}\right]$. Negligibility of the asymptotic values shown determines the validity of the risk-dominance inequality, according to Theorem 1.

Convergence of the risk-dominance quadratic coefficients can be quantified as in Figures 1 and 2, the continuation of which Table 1 summarizes.

Table-1: Convergence of the risk-dominance quadratic coefficients evaluated as N increases, according to (6). Selection intensity $\sigma = 1$. For the coefficients α^2, β^2, δ^2, $\alpha\gamma$ and $\alpha\delta$ the population sizes shown correspond to minimum 90% and 95% of their asymptotic values. Note coefficient equivalences occur such that $\beta^2 = 2\gamma\delta$, $\delta^2 = 2\alpha\beta$, $\alpha\gamma = \beta\delta$ and $\beta\gamma \equiv -\frac{1}{2}$. Note that $\alpha\delta$, $\beta\gamma$ and $\beta\delta$ have negative valued coefficients. Note also the coefficient of γ^2 converges from above; maximum 110% and 105% of its asymptotic value at the population sizes shown.

$\widetilde{N}(\alpha^2)_{-10\%}$	$\widetilde{N}(\beta^2)_{-10\%}$	$\widetilde{N}(\gamma^2)_{+10\%}$	$\widetilde{N}(\delta^2)_{-10\%}$	$\widetilde{N}(\alpha\beta)_{-10\%}$	$\widetilde{N}(\alpha\gamma)_{-10\%}$	$\widetilde{N}(\alpha\delta)_{-10\%}$	$\widetilde{N}(\gamma\delta)_{-10\%}$
52	14	14	27	27	20	39	14
$\widetilde{N}(\alpha^2)_{-5\%}$	$\widetilde{N}(\beta^2)_{-5\%}$	$\widetilde{N}(\gamma^2)_{+5\%}$	$\widetilde{N}(\delta^2)_{-5\%}$	$\widetilde{N}(\alpha\beta)_{-5\%}$	$\widetilde{N}(\alpha\gamma)_{-5\%}$	$\widetilde{N}(\alpha\delta)_{-5\%}$	$\widetilde{N}(\gamma\delta)_{-5\%}$
106	28	28	54	54	40	79	28

The precision of Table 1 corresponds to absolute errors in small magnitude coefficients and therefore represents conservative convergence thresholds.

3.2 Violation of the '1/2-rule' from non-harmful contests

Recall from Section 2.2, where the polarity of the second order term in (3) was positive according to Corollary 1.1. Consider the payoff matrix (1) in which the number of pairwise comparisons $\binom{4}{2} = 6$. The design of the game as a trade-off between cooperation and defection yields the following constraints: (i) $\alpha > \delta$; (ii) $\delta > \beta$; (iii) $\gamma > \delta$; (iv) $\gamma > \alpha$; (v) $\alpha > \beta$; and (vi) $\gamma > \beta$. Condition (i) prescribes the game as a social dilemma, and (ii) represents non-harmful contests. Condition (iii) prescribes rivalry between defectors that causes a reduced payoff due to their competitive interaction. Condition (iv) prescribes the exploitative gain of defectors against cooperators. Condition (v) prescribes the cost cooperators suffer due to the loss of cooperation when they encounter a defector. Condition (vi) prescribes the gain of defectors compared to the loss of cooperators from dissimilar strategy encounter.

Define three constants, $0 \leq c_1, c_2, c_3 \leq 1$, such that condition (iii) implies $\delta = c_3\gamma$, (iv) $\alpha = c_1\gamma$, and (vi) $\beta = c_2\gamma$. Furthermore, conditions (i) and (ii) imply $c_1 > c_3 > c_2$. Substitution into the deterministic equilibrium relative frequency of cooperation $\frac{\delta - \beta}{\alpha - \beta - \gamma + \delta} = \frac{c_3 - c_2}{c_1 - c_2 - 1 + c_3} \Rightarrow c_1 + c_3 > 1$, when $c_2 = 0$. Note also the risk-dominance inequality may be written $c_1 + c_2 > 1 + c_3$, which yields the contradiction $c_1 - c_3 > 1$, when $c_2 = 0$. This contradiction implies linear truncation error must exist in derivation. These non-negligible higher order terms were quantified in Figure 3.
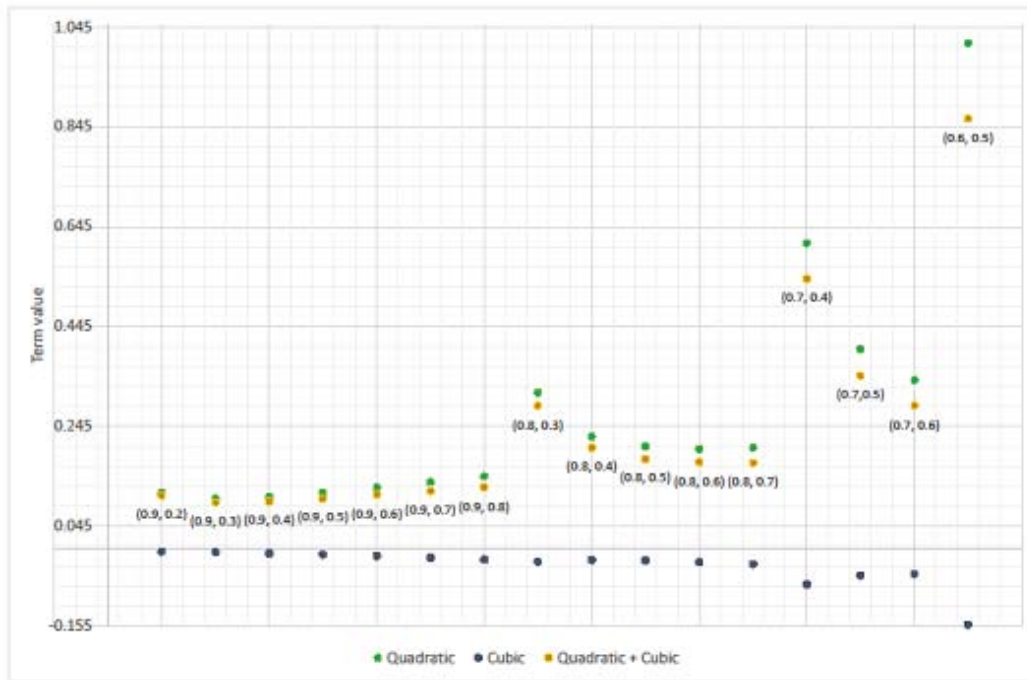
Figure-3: Quantified quadratic (second order) and cubic (third order) terms in the '1/2-rule' extension, via inequality (3) of Theorem 1. Non-negligible sums, quadratic plus cubic terms, were also quantified. Setting $\beta = 0$ and $\gamma = 1$ simplified the plot in two-dimensions, without loss of generality. Values in parentheses (c_1, c_3), increments of 0.1 from left to right, where $0 < c_1, c_3 < 1$ such that $c_1 > c_3$, or equivalently $\alpha > \delta$. Necessarily $c_1 + c_3 > 1$ ensures non-degenerate deterministic equilibrium relative frequency of cooperation. Selection intensity $\sigma = 1$. Horizontal axis represents term value zero.

Hence, according to Corollaries 1.1-2, only non-harmful contests yields violation of the rule.

4. CONCLUSION

Theorem 1 can be used to calibrate selection such that the risk-dominance inequality remains a reasonably valid first order truncation. Corollaries 1.1-2 show that weak selection does not always preserve risk-dominance, although the corresponding inequality holds in a reduced domain of the payoff matrix. When $\alpha < \gamma$ and $\beta < \delta$ defectors dominate. In this case, the reduced domain proven was such that $\frac{1}{2}\gamma < \alpha$ yields violation of the risk-dominance inequality due to additional non-negligible terms. Equivalently, the deterministic relative frequency of co-operation does not equilibrate to less than ½. Thus, preservation of the rule required exploitation of cooperators by defectors that exceeds doubled payoff. Therefore, exploitation must be escalated to preserve this evolutionary rule when defectors dominate. Otherwise, when $\beta > \delta$, violations of the rule were proven non-existent.

Derived inequality (4) will enable quantification of error thresholds due to second and third order terms as values of the payoff matrix entries vary when the selection differential between game strategies $\varpi \sim N^{-(1+p)}$, where $0 \le p \le 1$. This sharpens the calibration of selection that was deduced previously [19]. Note that first derivatives of one singleton fixation probability $\rho'_C(\varpi)$ and the quotient of singleton fixation probabilities $[\rho_C(\varpi)/\rho_D(\varpi)]'$ ([19], equations 2.6-9 and 3.4) convert by insertion of an inner summation within each resultant term of the requisite derivatives of the quotient; refer to (5) herein. Higher order derivatives do not convert similarly, due to additional components in the singleton fixation probability absent from the quotient derivatives.

Generalization of risk-dominance to multi-player games [3] must account for negligible singleton fixation probabilities in at least second order Maclaurin series. Generalizations of risk-dominance may exist within graphical spatially structured populations and their effects on fixation probabilities ([6], [12]).

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