

COOPERATION IN FINITE POPULATIONS: BEING ALONE HELPS

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ABSTRACT. We consider the evolution of cooperation in finite populations and we model a scenario where two individuals can interact only if both intend to do so with their counterpart. This feature allows a possibility for individuals to remain alone for a given round and not interact with anybody. Such an individual receives a baseline payoff rather than one based upon a matrix game. We provide sufficient conditions on the payoff matrix that will guarantee fixation probabilities to be monotone relative to the baseline payoff. We then apply the findings to the Prisoner's Dilemma and Hawk-Dove games. In both cases, the possibility that an individual might remain alone increases the chances that cooperation or non-aggression fixes within the population. Moreover, weak selection models overlap with our model, and we consider how one can generalize our model even further.

1. INTRODUCTION

The question of how natural selection can lead to cooperative behavior has fascinated evolutionary biologists for several decades [22] and mathematicians have created many models to answer the question. Until recently, most models considered deterministic dynamics in infinite populations, see for example [19, 15, 16, 17, 9]. Nevertheless, stochastic evolutionary dynamics in finite population is also well established, see for example [20, 21, 11, 24, 30]. One can consider stochastic models either in well mixed populations as in [29, 23], or more generally in structured populations as in [18, 4, 1]. All such models have been successfully applied to better understanding of the conditions for the evolution of cooperation, most notably through the Prisoner's Dilemma game [2] such as in [25], and Hawk-Dove game [19] such as in [14, 5].

In this paper, we consider the evolution of cooperation in finite populations where interactions might be avoided. In Section 2 we adapt the general framework of [7] to model a scenario where two individuals can interact only if they both intend to interact with one another. This allows a possibility that individuals may remain alone and do not interact with anybody, thereby receiving a default payoff rather than a payoff derived from a matrix game. In Section 3 we provide general conditions on the payoff matrix that will guarantee fixation probabilities to be monotone with respect to the baseline payoff. We then apply these findings to the Prisoner's Dilemma game in Section 4 and the Hawk-Dove game in Section 5. We

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conclude with a discussion of both the connection between our results and classical models involving weak selection and also how one can further generalize the model.

2. MODEL

Consider a finite population of $N \geq 3$ individuals that exhibit one of two behavioral types, labeled A and B . The individuals interact in pairwise fashion and thereby earn payoffs (reproductive fitness) which then drives the evolution of trait frequencies according to a standard Moran process [21]. At each time step, an individual is chosen for reproduction in proportion to its relative fitness. The offspring - identical to the parent - replaces another randomly chosen individual in the population. Thus the total population size remains constant.

We are interested in the fixation probability of trait A when it is initially rare (1 individual) amidst a population of $N - 1$ type B individuals. As in [29, 1], the interactions are modeled as a symmetric 2×2 game with a payoff matrix

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

where a is the payoff to a type A individual when it interacts with another type A individual, b is the payoff to a type A individual when it interacts with a type B individual, and so forth. In classical models such as [29, 18], every individual would receive an average payoff from all possible interactions; specifically, if there are i type A individuals, then a type A individual would receive

$$f_i = \frac{1}{N-1}(a(i-1) + b(N-i)), \quad (2)$$

because the individual can interact with any of the remaining $(i-1)$ type A individuals and any of $(N-i)$ type B individuals. Similarly, a type B individual would receive

$$g_i = \frac{1}{N-1}(ci + d(N-i-1)). \quad (3)$$

In our current model, we introduce a phase at the start of each time step wherein individuals uniformly randomly select a potential interaction partner. For individual I , we denote this potential partner as $T(I)$. If $I = T(T(I))$, then both individuals have agreed to interact and the individuals receive those payoffs assigned by (1). Mutual agreement happens with probability $\frac{1}{N-1}$. If individual I does not find a partner in a given round, which occurs with probability $\frac{N-2}{N-1}$, then individual I receives a default payoff α . Consequently, when there are i type A individuals in a population of size N , the average payoff for type A individuals is

$$F_i = \frac{1}{N-1}f_i + \frac{N-2}{N-1}\alpha, \quad (4)$$

and for type B individuals the payoff is

$$G_i = \frac{1}{N-1}g_i + \frac{N-2}{N-1}\alpha. \quad (5)$$

Considering first the individual fitness given directly by the payoffs f_i and g_i , we can calculate the fixation probability for an initially rare trait A as in [29] by

$$\rho_A = \frac{1}{1 + \sum_{j=1}^{N-1} \prod_{k=1}^j \frac{g_k}{f_k}}. \quad (6)$$

In the current model with payoffs F_i and G_i , the fixation probability of trait A becomes

$$\varrho_A = \frac{1}{1 + \sum_{j=1}^{N-1} \prod_{k=1}^j \frac{G_k}{F_k}}. \quad (7)$$

Following [29], a probability of fixation of behavioral type B when it is initially rare (1 individual) is given by the related formula

$$\rho_B = \rho_A \prod_{k=1}^{N-1} \frac{g_k}{f_k} \quad (8)$$

and similarly,

$$\varrho_B = \varrho_A \prod_{k=1}^{N-1} \frac{G_k}{F_k}. \quad (9)$$

For fixed values of a, b, c , and d , the fixation probabilities ϱ_A and ϱ_B are scalar functions of α with $\rho_A = \varrho_A(0)$ and $\rho_B = \varrho_B(0)$.

3. MAIN RESULT

Theorem 3.1. *For any given non-negative payoff matrix (1) that resolves interactions in a population with N individuals, if either the pair of conditions*

$$b - d < a - c, \text{ and} \quad (10)$$

$$c > \frac{1}{N-1}(a(N-2) + b), \quad (11)$$

or the pair of conditions

$$b - d > a - c, \text{ and} \quad (12)$$

$$b < \frac{1}{N-1}(d(N-2) + c), \quad (13)$$

hold true, then the fixation probability ϱ_A is increasing in α while ϱ_B is decreasing in α . Moreover, for $\alpha > 0$, fixation probabilities for initially rare types are well ordered, with

$$\rho_B > \varrho_B > \frac{1}{N} > \varrho_A > \rho_A. \quad (14)$$

Proof. Let $h(i) = (g_i - f_i)(N-1) = ci + d(N-i-1) - a(i-1) - b(N-i)$. This is a linear function of i , and its slope is

$$\frac{dh}{di} = (b-d) - (a-c). \quad (15)$$

If condition (10) is satisfied, h is strictly decreasing and the minimum value of h occurs when $i = N-1$. This value is

$$h(N-1) = c(N-1) - a(N-2) - b \quad (16)$$

which is positive under condition (11). Similarly, if (12) is satisfied, h is strictly increasing, and the minimum of h occurs at $i = 1$. The minimum value

$$h(1) = c + d(N-2) - b(N-1) \quad (17)$$

is positive under condition (13). Thus under either pair of conditions, $h(i) > 0$ for all $1 \leq i < N$.

Now, consider $H_i = \frac{G_i}{F_i}$. It follows that under conditions (10) and (11) (or (12) and (13))

$$\frac{dH_i}{d\alpha} = -\frac{(N-2)}{(N-1)} \frac{h(i)}{(f_i + (N-2)\alpha)^2} < 0. \quad (18)$$

Thus, by (7), $1/\varrho_A$ is decreasing in α , or equivalently stated, ϱ_A is increasing. In like manner, we can conclude that ϱ_B is decreasing. Furthermore, as the default payoff increases, the relative fitness of all individuals approaches the same value regardless of type, $\lim_{\alpha \rightarrow \infty} \frac{G_i}{F_i} = 1$. Selection is neutral in this instance, and the probability of fixation for a rare type is $1/N$. Consequently,

$$\rho_B > \varrho_B > \lim_{\alpha \rightarrow \infty} \varrho_B = \frac{1}{N} = \lim_{\alpha \rightarrow \infty} \varrho_A > \varrho_A > \rho_A. \quad (19)$$

□

By similar arguments as Theorem 3.1, one could also show that if (10) held true while (13) was false (or (12) and (11), respectively), then ϱ_A would be non-increasing in α with $\varrho_A < \rho_A$.

4. PRISONER'S DILEMMA

First we apply Theorem 3.1 to the Prisoner's Dilemma game, which has the payoff matrix

$$\begin{array}{cc} & \begin{array}{c} C \quad D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R & S \\ T & P \end{pmatrix}. \end{array} \quad (20)$$

In this game, strategy C is cooperation, and D is defection. It is assumed that $T > R > P > S$, see e.g. [2], where T is the temptation to defect, R is the reward for a pair of cooperators, P is the punishment for a defecting pair, and S is the sucker payoff for a cooperator being exploited by a defector.

For such payoffs, (11) and (13) are necessarily true since

$$\frac{1}{N-1}(P(N-2) + T) > \frac{1}{N-1}(P(N-2) + P) = P > S, \quad (21)$$

and also

$$\frac{1}{N-1}(R(N-2) + S) < \frac{1}{N-1}(R(N-2) + R) = R < T. \quad (22)$$

Thus either (10) and (11) or (12) and (13) must be satisfied. Consequently, $\varrho_C > \rho_C$ for all α , and cooperators are more likely to go to fixation if they are allowed to be alone. See Figure 1.

5. HAWK-DOVE GAME

Now we apply Theorem 3.1 to the Hawk-Dove game defined by the payoff matrix

$$\begin{array}{cc} & \begin{array}{c} H \quad D \end{array} \\ \begin{array}{c} H \\ D \end{array} & \begin{pmatrix} \frac{V-C}{2} & V \\ 0 & \frac{V}{2} \end{pmatrix}. \end{array} \quad (23)$$

H stands for a Hawk, or an aggressive individual, while D stands for a Dove, or a passive/cooperative individual. V is a reward for which the individuals fight, and C is the cost of the aggressive contest. In its traditional form, the cost of an aggressive fight outweighs the value of the resource, $C > V$; however, the matrix

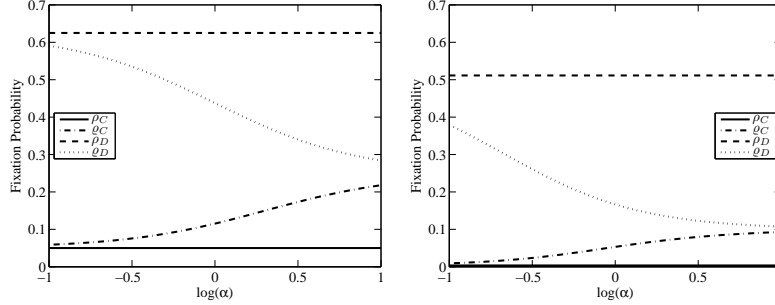


FIGURE 1. Fixation probabilities for the Prisoner's Dilemma game. Here $T = 5, R = 4, P = 2, S = 1$. (a) $N = 4$, (b) $N = 10$.

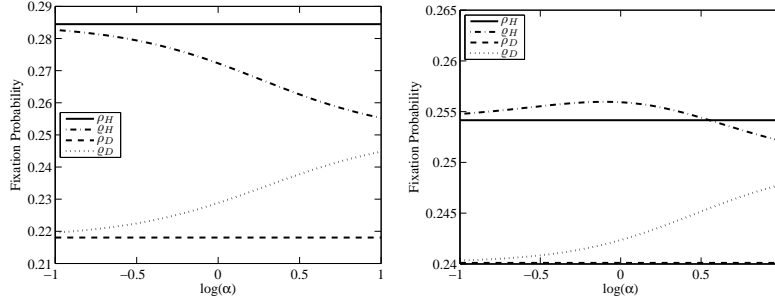


FIGURE 2. Fixation probabilities for the Hawk-Dove game. Here $N = 4, V = 1, c_0 = 3$. (a) $C = 3$, (b) $C = 4.7$.

(1) presumes non-negative entries. We may add a positive constant c_0 to all entries of the matrix (23) to ensure this condition, but this transformation has no effect on conditions (10)-(13). Since

$$V - \frac{V}{2} > \frac{V - C}{2}, \quad (24)$$

condition (12) is satisfied. If $C < \frac{N}{N-2}V$, then

$$0 < \frac{1}{N-1} \left(\frac{V-C}{2}(N-2) + V \right) \quad (25)$$

and condition (11) is not satisfied. Consequently, $q_H < \rho_H$ and q_H decreases with α while $\rho_D < q_D$ and q_D decreases with α . Note that

$$V > \frac{1}{N-1} \left(\frac{V}{2}(N-2) + 0 \right), \quad (26)$$

so condition (13) is never satisfied. Consequently, if $C > \frac{N}{N-2}V$, then Theorem 3.1 is no longer applicable. Moreover, for large C , q_H can be increasing for some range of α and decreasing for other values of α as seen in Figure 2. We can see that being alone helps Doves gain greater fixation probability.

6. DISCUSSION

We considered the evolution of cooperation in a finite population in a scenario where two individuals can interact only if both intend to interact with one another. Those individuals that did not interact with another individual receive a baseline payoff rather than always receive a payoff based on a matrix game.

Many models of evolution in finite populations (see [18, 25] but also counter-examples [6, 13]), consider weak selection where fitnesses f_i and g_i are transformed into $\tilde{F}_i = 1 + wf_i$ and $\tilde{G}_i = 1 + wg_i$. These models then consider the dynamics and fixation probabilities that such fitness functions have in the limit of $w \rightarrow 0+$. If $w = \frac{1}{(N-2)\alpha}$, then $\frac{G_i}{F_i} = \frac{\tilde{G}_i}{\tilde{F}_i}$ and so the fixation probabilities in weak selection corresponds to fixation probabilities in our model. Unlike models of weak selection, our model allows the study of more general situation when the individuals differ not only in the interactions but in the baseline fitness.

Our approach can be seen as a special case of a general framework from [7], and also [10, 5]. In this interpretation, we may view individuals as occupants of vertices of a complete graph that pick an edge to an adjacent vertex as a potential place to meet and interact with a neighbor. We considered that the meeting places are picked uniformly at random; however it is possible to incorporate some preference or location bias in selecting an edge. This variation of the model mirrors studies in [3, 28, 12].

By considering individuals as occupants on a general graph, our model extends naturally to structured populations. A further development would allow the interactions and baseline fitness to vary by individual and location. Since a population structure has a profound effect on the fixation probability [8], it will therefore be interesting to study the dynamics on a general population structure. Once we extend our model there, it will also be important to study various updating rules, e.g. [13, 27] as they are same as the Moran process in the homogeneous population but differ from the Moran process in general [26].

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