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The Donation Game with Roles Played Between Relatives

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Abstract

We consider a social game with two choices, played between two relatives, where roles are assigned to individuals so that the interaction is asymmetric. Behaviour in each of the two roles is determined by a separate genetic locus. Such asymmetric interactions between relatives, in which individuals occupy different behavioural contexts, may occur in nature, for example between adult parents and juvenile offspring. The social game considered is known to be equivalent to a donation game with non-additive payoffs, and has previously been analysed for the single locus case, both for discrete and continuous strategy traits. We present an inclusive fitness analysis of the discrete trait game with roles and recover equilibrium conditions including fixation of selfish or altruistic behaviour under both behavioural contexts, or fixation of selfish behaviour under one context and altruistic behaviour under the other context. These equilibrium solutions assume that the payoff matrices under each behavioural context are identical. The equilibria possible do depend crucially, however, on the deviation from payoff additivity that occurs when both interacting individuals act altruistically.

Keywords

evolutionary game theory, 2 x 2 games, kin selection, donation game, synergistic effect

Introduction

Social behaviour is often considered in its simplest form as an interaction between two individuals, each of which can exhibit two alternative behaviours. It is assumed that the two individuals' choices are made independently, and that each receives a payoff from the game according to their own action and that of the other. Such a game can be written in its most general form as a payoff matrix of the following form (table 1).

Grafen (1979) labelled the above payoff matrix the 'Hawk-Dove' game, not to be confused with the particular instantiation of the above payoff matrix labelled 'Hawk-Dove' by Maynard Smith (Maynard Smith & Price, 1973; Maynard Smith, 1982). By choosing different parameters A , B , C and D in this game a variety of social dilemmas can be realised (Rapoport & Guyer, 1966; Rapoport, 1967), including the widely studied Prisoner's Dilemma and Snowdrift games. The study of such social dilemmas between related individuals has attracted much attention since the introduction of the concept of inclusive fitness (Hamilton, 1964a; 1964b). Inclusive fitness theory considers altruistic interactions between individuals, where altruism is defined as incurring a fitness cost c to the altruist, while providing a fitness benefit b to the recipient. This is often referred to as the donation game. In fact, more general social interactions can be considered by allowing costs c or benefits b to be negative, such as weak altruism (c is negative, hence 'altruism' also increases personal fitness (Wilson, 1979) and even spite (b is negative, hence 'altruism' actually decreases the recipients' personal fitness (Hamilton, 1970). In this paper, we limit ourselves to the simple donation game with positive c and b , corresponding to strong altruism (c is positive, *ibid.*).

If altruism is under genetic control, and if some population structure exists such that genetically similar individuals interact with each other more frequently than they interact with individuals drawn uniformly at random from the entire population (e.g. Grafen, 1979), then altruistic behaviour is selected for whenever Hamilton's rule is satisfied (Hamilton, 1964a; 1964b):

$$r > \frac{c}{b}, \quad (1)$$

where r is the average degree of relatedness between interacting individuals.

Games having the form shown in table 1 played between relatives have been analysed both for populations of fixed strategy individuals, and populations of individuals whose strategy is a probability of playing each of the two game alternatives. Different strategy equilibria have been demonstrated for each situation (Grafen, 1979).

By defining

$$-c = B - D, \quad (2a)$$

$$b = C - D, \quad (2b)$$

and

$$d = A - B - C + D, \quad (2c)$$

and by transforming the payoffs such that $D = 0^1$, the payoff matrix in table 1 can be rewritten as table 2 below (Queller, 1984).

¹ game theoretic equilibria are invariant under such a payoff matrix transformation (e.g. Weibull, 1995, p. 73)

Table 2 is the payoff matrix for the synergistic donation game in which each individual can decide whether to behave altruistically (choose **I**) or not (choose **II**). Note that for strong altruism we require that $b, c > 0$, as described above. One important point is that there is a deviation from payoff additivity d , also known as the synergistic effect, that occurs when both individuals behave altruistically towards each other. The game payoffs A, B, C and D can be chosen such that $d = 0$ (payoffs are additive), $d < 0$ (payoffs are negatively non-additive), or $d > 0$ (payoffs are positively non-additive), while still maintaining $b, c > 0$. Deviation from payoff-additivity has implications for the application of Hamilton's rule. For the synergistic donation game played in a population of relatives with deterministic strategies, the population strategy at equilibrium depends both on relatedness r and on deviation from additivity of payoffs d . If relatedness is sufficiently high or low, or if payoffs are additive ($d = 0$) altruistic (type **I**) or selfish (type **II**) behaviour will take over the population. However if relatedness is intermediate and payoffs are non-additive ($d \neq 0$) then a polymorphic population equilibrium which is either stable ($d > 0$, *i.e.* positively non-additive payoffs) or unstable ($d < 0$, *i.e.* negatively non-additive payoffs) results (Queller 1984).

Games With Roles Played Between Relatives

Analyses of the 2×2 games, and the donation game in particular, often assume a symmetric interaction in which both players have opportunities to donate altruistically towards the other, and do so using a common decision rule. However in nature many typical social interactions are not symmetric, but individuals may interact under different behavioural contexts, making use of different rules to determine behaviour in each context (e.g. Maynard Smith & Parker, 1976; Selten, 1980; 1983,

Hammerstein, 1981; Maynard Smith, 1982). It is then interesting to consider such interactions between relatives. For example, in a potentially altruistic interaction between an adult and offspring each individual may occupy different behavioural contexts, and hence use different rules to decide on altruistic behaviour, through differences in individuals' state variables such as energy reserves and body mass, possession of a territory, and so on. In such situations it may provide an inclusive fitness benefit to an individual to behave altruistically in one context, but not in another. Maynard Smith & Parker (1976) have also noted that one need not assume differences in payoffs under the different contexts for such equilibria, as one would expect if individuals' states did indeed differ, but that 'uncorrelated asymmetries' having the same outcome can occur when the payoff matrices are identical for each individual. In the remainder of this paper we will examine conditions for 'uncorrelated asymmetries' to occur in the donation game with roles played between relatives.

The Donation Game with Roles and Relatedness

For the model described below we will adopt the usual 'phenotypic gambit' (Grafen, 1984), and assume that each behaviour is under independent genetic control by a haploid locus. We consider the game defined by the payoff matrix of table 1, which as noted above can be mapped onto the donation game with potentially non-additive payoffs as presented in table 2. We assume discrete, deterministic strategies. Thus far, our model is entirely the same as the discrete trait models considered by Grafen (1979) and Queller (1984). We now make two modifications to these previous approaches: first, by considering two distinct behavioural contexts, with action under each being subject to a separate genetic locus. These two contexts are mutually

exclusive for any given interaction, so when two players interact each must occupy a different behavioural context, and thus use different loci to determine their behaviour for the interaction. We consider a population in which individuals in one role have type **I** (hereafter called *altruistic*) behaviour at population frequency g , and type **II** (hereafter called *selfish*) behaviour at population frequency $(1 - g)$. We model the inclusive fitness of altruistic and selfish behaviour to determine the change in g over time, given that these individuals encounter altruistic behaviour in opponents occupying the other role at the population frequency f , and selfish behaviour at population frequency $(1 - f)$. A similar calculation is done for the change in f over time, given g . Second, to model the inclusive fitness component of the interaction, the payoff the opponent receives from the interaction is included in the fitness calculation, weighted by the degree of relatedness r for interactions within the population. We shall not consider the frequency with which individuals in the population experience each behavioural context. Rather, we shall write down inclusive fitness equations for the alleles for altruistic (type **I**) and selfish (type **II**) behaviour in each context, and solve for fitness inequality. Subsequently we shall examine the relationship between selection pressure at these two behavioural loci using the replicator dynamics. Under the above model, these equations for a single behavioural context are

$$w_I = Af + B(1 - f) + r(Af + C(1 - f)), \quad (3a)$$

and

$$w_{II} = Cf + D(1 - f) + r(Bf + D(1 - f)), \quad (3b)$$

where, as described above, r is relatedness for the locus in question, and f is the population frequency of altruistic behaviour at the locus for the other behavioural

context. In equations 3a and 3b above the first two terms give the expected payoff to the focal individual, and the last term is the expected payoff to the opponent, weighted by the focal individual's relatedness to them. The above inclusive fitness equations avoid double-counting the fitness effects of genes (Grafen, 1982; 1984), as fitness benefits of genes at two distinct loci are considered (cf. Queller, 1996).

There are two important quantities of interest to solve for in considering when altruistic and selfish behaviours have equal fitness. If we solve $w_I = w_{II}$ for the critical relatedness threshold r' above which altruistic behaviour is favoured by selection we have

$$r' = -\frac{f(A-B-C+D)+B-D}{f(A-B-C+D)+C-D}. \quad (4)$$

Through rewriting using equations 2a-2c this gives a synergistic version of Hamilton's rule

$$r' = \frac{c - fd}{b + fd}, \quad (5)$$

which is the equivalent for our discrete donation game with roles of Queller's (1984) equation 5b for the discrete donation game without roles. If payoffs are additive ($d = 0$) then equation 5 reduces to Hamilton's rule, however as discussed in Queller and above positively non-additive payoffs ($d > 0$) make altruism easier to select for than predicted by Hamilton's rule, while for negatively non-additive payoffs ($d < 0$) altruism is harder to select than Hamilton's rule predicts. In both cases the relatedness threshold for altruism varies non-linearly as a function of frequency of altruism in the population under the other behavioural context.

If instead we solve $w_I = w_{II}$ for the population frequency of altruistic behaviour in the other, opponent's, context above which altruistic behaviour will be favoured in the current behavioural context, then we have

$$f' = \frac{D - B - r(C - D)}{(1 + r)(A - B - C + D)}. \quad (6)$$

Intriguingly, this is identical to Grafen's equilibrium frequency for altruism in the continuous 'Hawk-Dove' game between relatives (Grafen, 1979, eq. 10), although here equation 6 above is actually the threshold frequency for altruistic behaviour under the opponent's behavioural context, above which altruistic behaviour at the focal individual's behavioural context will be selected for. Rewriting using equations 2a-2c, equation 6 can be expressed in terms of fitness costs, benefits and synergistic effects as

$$f' = \frac{c - rb}{(1 + r)d}. \quad (7)$$

It is easy to examine the fixed points of selection at the loci determining behaviours in both roles by substituting equations 3a and 3b into the replicator dynamics (Schuster & Sigmund, 1983), so we consider change in frequency of altruistic behaviour for the focal individual's behavioural context, g , as

$$\dot{g} = g(w_I - (gw_I + (1 - g)w_{II})). \quad (8)$$

Equations 3 to 8 all refer to selection operating on one of the behavioural contexts. By symmetry, equations for the other behavioural context are obtained by simply exchanging f for g and vice-versa throughout. This gives an equation for \dot{f} , the change in f over time, that is the counterpart of equation 8, allowing us simultaneously to consider the change in g and f over time.

The equilibria of equation 8 are, of course, where $g = 0$, $g = 1$, and $w_I = w_{II}$. In all cases this last equilibrium will be unstable. Selection of the remaining two equilibria according to the replicator dynamics will depend on relative costs c and benefits b of altruism, the relatedness r in the population, and the synergistic effect d . Figures 1 to 3 show numerically calculated sample dynamics of equation 8 (and its counterpart for \bar{X}), for representative values of these parameters. If ratio of cost to benefit is sufficiently high, or low, relative to population relatedness, then at both behavioural contexts alike altruistic or selfish behaviour will go to fixation regardless of population state, just as in the standard donation game with additive payoffs (e.g. figure 1). If, however, the synergistic effect is non-zero, and if population relatedness is at an intermediate value, such that it falls between the extrema of equation 5, then more interesting dynamics are observed. If the synergistic effect d is negative, then selective pressures act to bring about a stable co-existence of an altruistic behaviour for one behavioural context and a selfish behaviour for the other behavioural context (figure 2). Which of these equilibria is selected will depend on the population frequencies of the two behaviours and the relative strength of selection at the two loci. Conversely, if the synergistic effect d is positive, then either fixation of altruistic behaviour under both contexts, or selfish behaviour under both contexts, is stable (figure 3). Again, which equilibrium is selected depends on population frequencies and relative strengths of selection for the two behaviours. The stability of the different equilibria is demonstrated in the Appendix A. These results agree with a derivation based on Maynard Smith's (1982) work, as demonstrated in Appendix B.

Discussion

Evolutionary game theory has been applied to the study of altruistic interactions between relatives where there may be a synergistic deviation from payoff additivity when two altruists interact (Grafen, 1979; Queller, 1984). In earlier models a single altruistic trait has been considered. In this paper we have examined the synergistic donation game played between relatives when each individual occupies a different behavioural context, and different altruistic traits govern behaviour under each behavioural context. In such games stable equilibria corresponding to fixation of altruistic behaviour under both contexts, or fixation of selfish behaviour under both contexts, are both possible according to payoffs and relatedness. Negatively non-additive payoffs and intermediate levels of relatedness however, induce a change in the stable equilibria of the population: negatively non-additive payoffs and a suitably intermediate relatedness result in stable pairings of altruism under one behavioural context, and selfishness under the other behavioural context. In contrast, positively non-additive payoffs with a suitably intermediate relatedness result in stable fixation of altruistic behaviour under both contexts, or stable fixation of selfish behaviour under both contexts. These results for the donation game with roles are analogous to results for the single trait case in which negatively non-additive payoffs induce stable polymorphic population equilibria, and positively non-additive payoffs induce unstable polymorphic population equilibria (Queller, 1984).

Situations in which individuals involved in an altruistic interaction do so under different behavioural contexts are likely to occur frequently in nature. For example, the use of state-dependent behavioural rules leads to such asymmetric interactions (e.g. Maynard Smith & Parker, 1976; Selten, 1980; 1983; Hammerstein, 1981; Maynard Smith, 1982; Houston & McNamara, 1999). We consider cases in which

payoffs and actions are the same from both players' points of view, but each player makes use of a different trait to determine their action. One particular example of when such situations can occur is during repeated interaction with memory, where both individuals base their decisions on the outcome of their previous interaction. If at one interaction one individual provides an altruistic benefit to the other, but receives nothing in return, then at the next interaction each individual has a different perspective: one individual has just exploited the other, while the other has just been exploited. Marshall & Rowe (2003) studied such games and concluded, based on the traditional Prisoner's Dilemma payoff matrix, that interactions between relatives could undermine selection for 'retaliatory' behaviour in the Iterated Prisoner's Dilemma, in which an individual responds to exploitation of the form just described above by behaving selfishly on the next interaction. Marshall & Rowe concluded that kin selection could thus undermine selection for conditionally cooperative strategies for repeated interactions, such as the famous Tit-for-Tat (Axelrod, 1984). The results presented here show that this effect is in fact due to the negatively non-additive nature of the traditional Prisoner's Dilemma payoffs, and that a variety of other outcomes could occur given additive or positively non-additive game payoffs.

Games played between relatives using different behavioural rules as they occupy different behavioural contexts are likely occur in many other situations in nature. Queller (1996) discussed conditional expression of traits based on state variables, such as in the example of a stronger individual monopolising the role of reproductive and relegating the weaker relative to the role of helper, and sketched an outline of our model by considering interactions in which individuals express different genes to make their game choices. We agree with Queller's observation that conditional

expression of traits is likely to be more common than unconditional expression due to the greater flexibility of the former strategy (see also Houston & McNamara, 1999). In cases such as the example of a stronger individual monopolising reproduction, differences in the resources of the individuals might well be expected to lead to different payoff matrices for the interactants. In such cases it is of course easy to envisage payoff matrices that induce one individual to behave selfishly and the other to behave altruistically, due to the different costs and benefits of altruism that would accrue to each. However Maynard Smith & Parker (1976) have pointed out that differences in payoffs are not necessary for such equilibria to arise, and that ‘uncorrelated asymmetries’ of the same form can arise even when the payoff matrices are the same for both interacting individuals. The scenario presented in Marshall & Rowe (2003) and outlined above is an example of just such an uncorrelated asymmetry. The contribution of this paper is an explicit analysis of how uncorrelated asymmetries can arise in donation games with roles played between relatives, in terms of a modified version of Hamilton’s rule. This analysis highlights the crucial importance of negative non-additivity of payoffs in such interactions. Given it seems likely that non-additive interactions occur frequently in nature, it is hoped that the results presented here will be of some value.

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Appendix A

We consider the stability of the various equilibria under the replicator dynamics (equation 7), which for ease of exposition can be written as

$$\dot{g} = (g - g^2)(w_I - w_{II}), \quad (\text{A1})$$

making clear that selection always acts in favour of the fittest allele, since as $g \in [0,1]$ then $g - g^2 \geq 0$.

Now it is easy to see that the $w_I - w_{II}$ equilibrium is unstable since, as $w_I - w_{II}$ does not depend on g and there can thus be no frequency dependent effects in g , an increase in the fitness of one allele will lead to runaway positive selection for that allele.

For the stability of the $f \in \{0,1\}, g \in \{0,1\}$ equilibria we first choose $f=0$. Then

$$w_I - w_{II} = rb - c, \quad (\text{A2})$$

which is positive when equation 1 is satisfied. So if $f=0$, then $g=1$ is stable iff $r > c/b$.

Next we choose $f=1$. Then

$$w_I - w_{II} = d - c + r(d + b), \quad (\text{A3})$$

which is negative when r is less than the r' given by equation 5 with $f=1$. So if $f=1$, then $g=0$ is stable iff $r < (c - d) / (b + d)$. By symmetry the same analysis can be applied (exchanging f for g and vice-versa throughout) to find the stability of the $f=0$ and $f=1$ equilibria.

Putting these conditions together, the $f=0, g=1$ and $f=1, g=0$ equilibria are bistable iff

$$\frac{c}{b} < r < \frac{c - d}{b + d}. \quad (\text{A4})$$

Conversely both the $f=0, g=0$ and $f=1, g=1$ equilibria are bistable iff

$$\frac{c-d}{b+d} < r < \frac{c}{b}. \quad (\text{A5})$$

Now assuming that we are considering strong altruism, so b and c are both positive, then

$$\frac{c}{b} < \frac{c-d}{b+d}. \quad (\text{A6})$$

iff $d < 0$. So the $f=0, g=1$ and $f=1, g=0$ equilibria are bistable iff inequality A4 is satisfied, which can only occur if $d < 0$ (payoffs are negatively non-additive), whereas the $f=0, g=0$ and $f=1, g=1$ equilibria are bistable iff inequality A5 is satisfied, which can only occur if $d > 0$ (payoffs are positively non-additive). Otherwise one of the $f=0, g=0$ or $f=1, g=1$ equilibria will be globally stable.

Appendix B

We show the relationship between the derivation of the results presented in this paper, and a derivation based on Maynard Smith's (1982, pp.123-126) 'uncorrelated asymmetries' approach.

We first assign values to Maynard Smith's payoff matrix (table B1) to reflect the inclusive fitness of type **I** and type **II** behaviour given the opponent's behaviour, based on equations 3a and 3b. If the opponent displays type **I** behaviour then $f=1$ in these equations, otherwise $f=0$. Thus the payoffs in the game are

$$\alpha = (1+r)A, \quad (\text{B1a})$$

$$\beta = C + rB, \quad (\text{B1b})$$

$$\chi = B + rC, \quad (\text{B1c})$$

$$\delta = (1 + r)D. \quad (\text{B1d})$$

Maynard Smith's condition for mutual type **I** behaviour to be an equilibrium is

$$\alpha > \beta, \quad (\text{B2a})$$

and

$$\chi > \delta, \quad (\text{B2b})$$

whereas mutual type **II** behaviour is an equilibrium if both of these inequalities are reversed. Maynard Smith referred to both of these equilibria as 'Type 1'.

Substituting equations B1a-B1d into equations B2a-B2b we find that both of these inequalities are identical if d (as defined in equation 2c) is 0; in other words if payoffs are additive. The resulting single inequality can then be rewritten using equations 2a and 2b for $-c$ and b respectively, and the fact that $d = 0$ to be exactly the same as equation 1; in other words, if payoffs are additive then fixation of altruistic or non-altruistic behaviour in both behavioural contexts is predicted by Hamilton's rule.

Maynard Smith's condition for type **I** behaviour at one context and type **II** behaviour at the other context to be an equilibrium is (labelled by Maynard Smith as a 'Type 2' equilibrium)

$$\alpha > \beta, \quad (\text{B3a})$$

and

$$\chi < \delta, \quad (\text{B3b})$$

whereas mutual type **I** behaviour or mutual type **II** behaviour is an equilibrium (labelled ‘Type 3’ by Maynard Smith) if both of these inequalities are reversed (N.B. the conditions for ‘Type 2’ and ‘Type 3’ appear to have been swapped erroneously in Maynard Smith (1982, p.124).

If inequalities B3a and B3b are satisfied then one can rewrite them using equations B1a-B1d and 2a-c and combine to give inequality A4, whereas if neither inequality is satisfied then we can rewrite as inequality A5. Thus the results of appendix A can also be derived using Maynard Smith’s results.

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Figure 1: Selection pressure on frequency of altruistic behaviour under first context (f) and second context (g) for additive payoffs and high relatedness ($b = 4, c = 2, d = 0, r = 0.6$)

Figure 2: Selection pressure on frequency of altruistic behaviour under first context (f) and second context (g) for negatively non-additive payoffs and intermediate relatedness ($b = 4, c = 1, d = -1, r = 0.5$)

Figure 3: Selection pressure on frequency of altruistic behaviour under first context (f) and second context (g) for positively non-additive payoffs and intermediate relatedness ($b = 4, c = 2, d = 1, r = 0.4$)

	I	II
I	A	B
II	C	D

Table 1. Payoffs for the general 'Hawk-Dove' game (payoffs to row player shown).

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	I	II
I	$b - c + d$	$-c$
II	b	0

Table 2. Payoffs for the donation game with potentially non-additive payoffs (payoffs to row player shown).

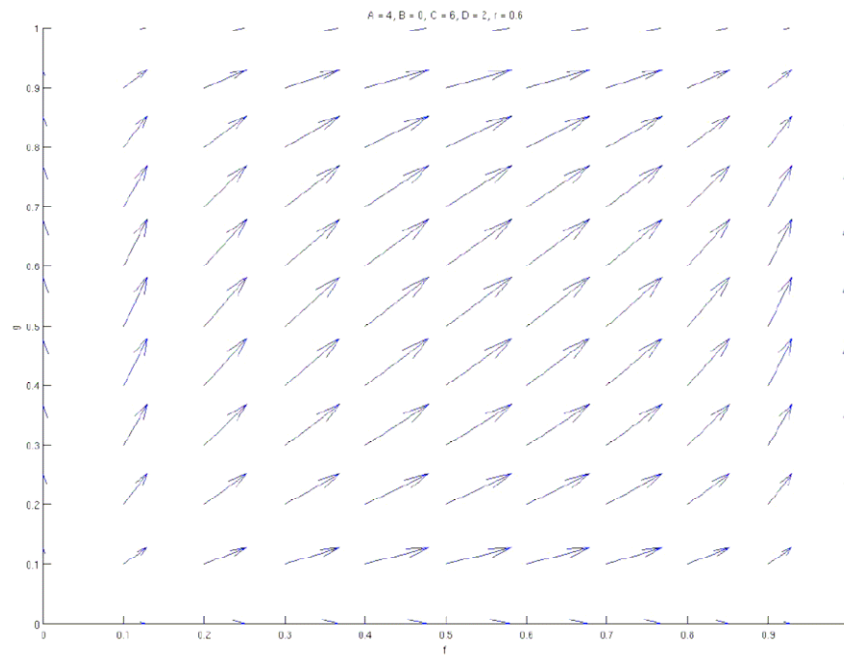
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	I	II
I	α	χ
II	β	δ

Table B1. Payoffs for the ‘uncorrelated asymmetry’ analysis (payoffs to row player shown).

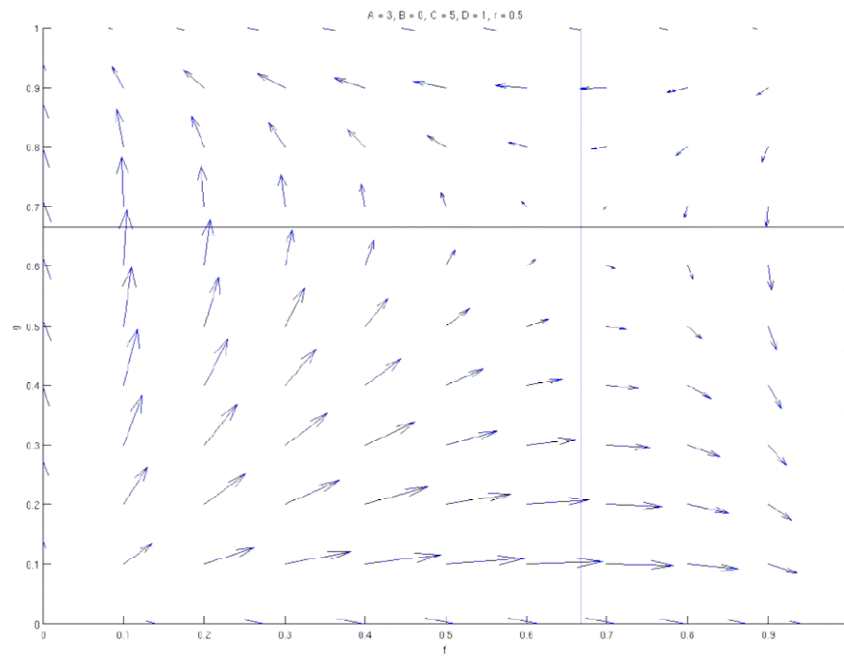
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Fig 1:



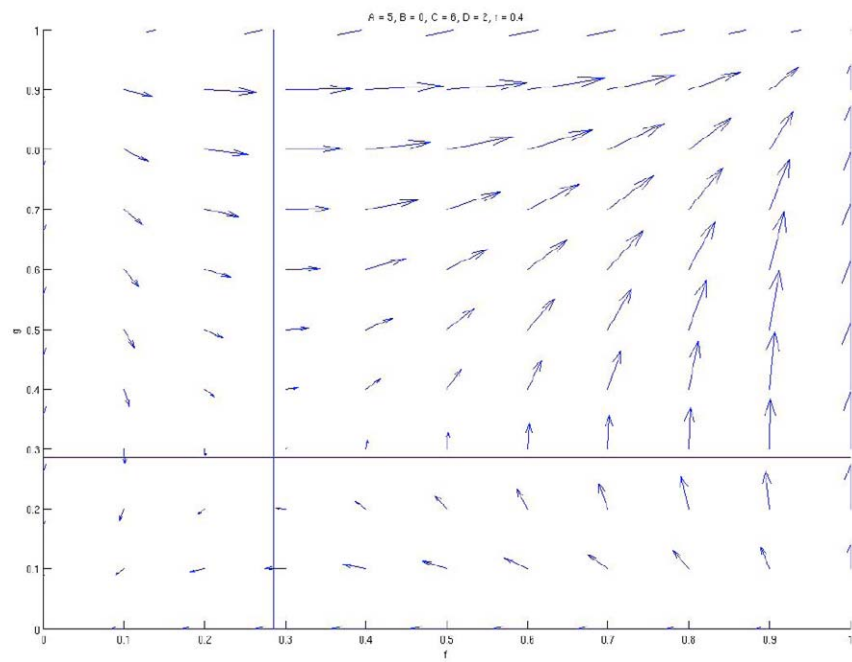
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Fig 2:



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Fig 3:



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