Evolution of Co-operation When the Strategies are Hidden: The Human Mating Game

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Defection is frequently seen in co-operative systems [1-3]. Game theoretical solutions to stabilize cooperation rely on reciprocity and reputation in iterated games[4-5]. One of the basic requirements for reciprocity or reputation building is that the strategies of players and the resulting payoffs should be open at the end of every interaction. For games in which the strategies and payoffs remain hidden, these stabilizing factors are unlikely to work. We examine the evolution of cooperation for hidden-strategy games using human mating game as an example**.** Here faithful parenting can be considered as cooperation and extra-pair mating (EPM) or cuckoldry as defection. Cuckoldry may get exposed only occasionally and the genetic benefits of cuckoldry also remain hidden from the players. Along with mate guarding, social policing is enabled in humans by language and gossiping. However, social policing can be invaded by second order free riders. We suggest that opportunistic blackmailing, which is unique to hidden strategy games can act as a keystone strategy in stabilizing co-operation. This can counteract free riding and stabilize policing. A game theoretical model results into a rock - paper – scissor (R-P-S) like situation with no evolutionary stable strategy (ESS). Simulations result into a stable or stably oscillating polymorphism. Obligate monogamy is an essential trait in the co-existence. In a gender difference model too, polymorphism is seen in both genders but with different traits predominating in the two genders. The model explains intra-gender, inter-gender as well as cross cultural variability in mating strategies in humans.

Introduction

Cooperation is commonly accompanied by cheating or defection in a number of naturally occurring social systems [1-3]. The problem of evolution and stability of cooperation between individuals is commonly addressed using a game theory model popularly known as Prisoner's Dilemma (PD). In a one time PD game, cooperation is not stable and defection is the only stable strategy for any player [4]. However, in iterated games strategies involving reciprocity or reputation can stabilize cooperation [4-5]. If the same individuals play the game again, defection can be retaliated [4]. Co-operators can build a reputation and derive long term gains from it [5]. Recent empirical [6] and theoretical [7, 8] studies emphasize that cooperation can evolve if co-operators punish those who defect. A potential problem in punishment is that there is a cost in executing punishment, which makes punishment an altruistic act. Since the benefits of punishing cheaters are shared, there arises a possibility of second order free riders that do not contribute to punishment but gain from it. The second order free riders can destabilize punishment and cooperation in turn. A number of conditional solutions to this problem have been suggested [7-9]. One of the basic assumptions behind all suggested solutions to the problem of stability of cooperation is that the strategies of players and the resulting payoffs are open at the end of every interaction. If players know the history of an individual player retaliation or punishment is possible. Public knowledge can help build reputation, which further enhances cooperation. Reciprocity and reputation would fail to work for games in which the strategies and payoffs remain hidden. If the players have a choice of secrecy or deception the outcome would be much different. We model the evolution of cooperation when the strategies and payoffs remain hidden most of the time.

The human mating system is an ideal and obvious example of hidden strategy games. In species where biparental care is necessary, faithful parenting can be considered as cooperation and extra-pair mating (EPM) or cuckoldry [10-17] as defection. Here, the polygamous or defecting individuals get an additional genetic advantage, but their mates have to bear a genetic loss. The nature of advantage obtained by males and females is qualitatively different. Males can increase their reproductive success quantitatively by gaining access to more females. Females, on the other hand, may not increase the number of offspring but may gain qualitatively through sperm competition or getting dual benefit of good parenting from one male and good genes from another [11, 18-22]. Cuckoldry is a hidden strategy and its genetic payoffs also remain hidden since players do not have a direct access to paternity information.

Two types of measures against cuckoldry are seen in the human society, namely mate guarding [17], a trait shared by many species [23-26] and punishment if cuckoldry gets exposed [27], a trait predominantly human. Although the probability of getting exposed is small its consequences are known to be severe in most human societies and exposed adulterous individuals generally receive punishment in some or the other form. Altruistic punishment or strong reciprocity has been used in the models of evolution of cooperation [5-7, 28]. However, altruistic punishment suffers from the problem of second order free riders [29]. In the human mating system there can be a non-altruistic punishment in the form of social sanctions. If an adulterous individual is deserted by its partner and makes the reason public, the probability of pairing again could be very small for the deserted individual owing to social sanctions. For the deserting partner, if the probability and benefit of pairing again is higher than continuing partnership with a defector, deserting would be a non-altruistic way of punishing. Avoiding pairing with a known defector is also a non-altruistic act. Therefore, punishment for cuckoldry in the form of social sanctions can be probabilistic but need not have an altruistic element in it.

In humans, due to evolution of language, gossip is possible through which one can gain information about the behaviour of a sexual partner in one's absence. This is an indirectly reciprocating, apparently altruistic social act that we will call 'social policing'. The cost involved in social policing can be substantially small as compared to individual mate guarding. However, as long as there is a cost of social policing some second order free riders can take advantage of the system. Individuals who do not contribute to social policing may still gain from it by getting information about their sexual partner. Such free riders can destabilize social policing. We suggest here that opportunistic blackmailing can give a solution to the problem. Since the strategies are hidden and exposure can lead to punishment, blackmailing is possible. When defection is exposed to only one or a few individuals the defector may give some form of direct benefits to the blackmailer and avoid social punishment. Since blackmailing necessarily depends upon differential secrecy, it is restricted to hidden strategy games. The success of blackmailing is highly conditional, but whenever the conditions favour blackmailing, it can give direct returns on investment in policing. Policing without blackmailing is an altruistic act and will be selected against in the presence of blackmailers. For a policing individual, the opportunities to blackmail increase with increasing investment in social policing. Since non-policing individuals are less likely to get a blackmailing opportunity, free riders are unlikely to thrive. All individuals engaged in EPM, on the other hand, have to bear a probabilistic penalty as a result of social sanctions or blackmailing.

Our model assumes a “marriage system” in which every individual player has to engage in a cooperative parenting act. In other words, all individuals are socially monogamous, but they can become genetically polygamous by engaging in EPM. Players have a choice to desert and probabilistically pair again with a random individual. Players are also allowed to deny pairing with individuals with a bad reputation. Individual players in the model can have alternative strategies on four different lines. Individuals can be (i) genetically monogamous (M^+) i.e. co-operators, or polygamous (M^-) i.e. defectors (ii) guarding (G^+) or non-guarding (G^-) (iii) policing (P^+) or non-policing (P^-) and (iv) blackmailers or non-blackmailers. Combinations of the above traits give 16 different strategies. However, policing without blackmailing is at an all time disadvantage as compared to policing blackmailers. On the other hand since the information necessary for blackmailing is acquired by policing, non-policing blackmailers cannot exist. This results into an obligate association between policing and blackmailing and leaves only 8 strategies in the game.

Results:

The payoff matrix (Table 1) shows that if the maximum probabilistic cost of punishment is greater than the advantage of polygamy, there is no ESS possible. This leads to a R-P-S like situation [Fig 1]. A monogamous, non-guarding, non-policing ($M^+G^-P^-$) strategy can be invaded by any of the polygamous (M^-) traits. Once a substantial proportion of the population is polygamous, guarding (G^+) and policing (P^+) become advantageous strategies. However, when majority of the population is $M^-G^+P^+$ the burden of punishment and blackmailing reaches its maximum. Therefore an $M^+G^+P^+$ trait can invade the population. With majority of individuals being monogamous, guarding and policing lose their relevance and the

$M^+G^-P^-$ trait invades the population since it does not pay these costs. This RPS like situation gives rise to a stable or oscillating polymorphism with obligate monogamy as an essential trait.

Simulations showed however, that the dynamics was more complex [Fig. 2 and 3]. For example, although $M^-G^+P^+$ was the fittest among the polygamous traits when the entire population was polygamous, when the population had a certain proportion of monogamous individuals, $M^-G^-P^+$ or $M^-G^+P^-$ enjoyed greater fitness then $M^-G^+P^+$. As a result of differential fitness advantages at different population composition, all the eight strategies could coexist in stable oscillations [Fig 2]. At high rates of punishment, oscillations dampened rapidly to give stable steady states with co-existence of all 4 policing traits [Fig 3a]. Stable or oscillating co-existence critically depended upon blackmailing. If the blackmailing benefit was reduced to zero, only polygamy with mate guarding prevailed [Fig 3b]. Stable steady states were obtained when the punishment was greater than a threshold [Fig 4].

The simulations were run with two sets of assumptions. In the first, no gender difference was assumed and therefore the model was equivalent to assuming that any individual randomly mated with any other. In the second, two genders were assumed and there was random pairing between individuals of opposite genders. Results of the two-gender model were identical to the non-gender model if parameters for both the genders were kept identical.

With different parameters for the two genders, we obtained differential outcome for males and females. For males, the genetic advantages of EPM as well as the genetic loss from partner’s EPM can be greater as compared to females. In many societies, the punishment for cuckoldry is more severe for females. It is also likely that males can get a higher benefit from blackmailing. The former differences are genetic whereas the later two are decided more by social norms. Introducing these differences in the model resulted into different proportions of traits in the two genders; nevertheless, polymorphism existed in both the genders (Fig. 5a and b).

Discussion:

All models for the evolution and stability of cooperation in a PD like game are dependent upon knowledge and memory of an individual's strategies in some way or the other. In reality there can be many situations where the players can hide their strategies. None of the known mechanisms for the stability of cooperation are likely to work under these conditions. It would appear therefore that cooperation couldn't be stable when the strategies are hidden. We show on the contrary that even if there is a small probability of exposure of the strategies, policing and cooperation can be stable. This depends critically on blackmailing that gives stability to policing. In open strategy games, on the other hand, blackmailing is not relevant and therefore the problem of free riders persists. Thus ironically, cooperation is more likely to be stable when the strategies are hidden.

Although our model is in the specific context of human mating system, it has more general implications. The necessary conditions for a general application of the model are that a non-altruistic punishment exists and blackmailing is possible. In all the previous models involving punishment, punishing is more effective when the frequency of defectors is low and that of punishers is high [5, 9]. As a result it is difficult for co-operators and punishers to invade defectors. In our model the opportunities of blackmailing increase with increasing frequency of defectors. This strengthens the invading power of policing traits and the model becomes more independent of the initial conditions. The benefits of policing decrease when majority of the population consists of co-operators. Such a negative frequency dependence, which is unique to this model as compared to all PD based cooperation models, makes co-existence of different strategies possible.

The model has important implications for the stability of monogamy and biparental care. The model shows that although mate guarding can counteract cuckoldry to some extent, it cannot stabilize monogamy. In the absence of social sanctions and blackmailing, opportunistic promiscuity with mate guarding is the only ESS. The model theoretically demonstrates for the first time that Darwinian mechanisms can make obligate monogamy stable in a population. Although there are advantages of occult promiscuity to both, males and females, the punishment and blackmailing cost is frequency dependent. Therefore a significant proportion of the population can remain obligately monogamous. Kale and Watve [27] showed similar stability earlier but their model involved altruistic punishment and results critically depended upon an unsubstantiated assumption that only mate guarding individuals contribute to social punishment. The blackmailing model makes altruism and any such assumptions unnecessary.

A popular critic of evolutionary psychology has been that it predicts gender specific stereotypes, whereas there are data for much intra-gender variation in human societies [16, 28]. Intra-gender variation has received much less theoretical attention than sex differences have [30]. Surprisingly the role of punishment and social policing is rarely appreciated [31, 32]. A good evolutionary model for human sex should be one that explains the universals as well as intra-gender, inter-gender and cross cultural differences [28, 30-33]. Classical sexual selection models are unable to do so and the theory of cooperative games is emerging as a promising alternative [34]. Unlike classical sexual selection models, in our model different strategies can coexist in the same gender and the predominant traits can be different in males and females. Furthermore some of the parameters are culture dependent and these factors can affect the resulting proportions of traits. Thus the model accommodates cross-cultural differences as well. The classical sexual selection theory holds that all individuals should be opportunistic defectors and if we see faithful monogamy in the population it must be owing to the lack of opportunities for EPM. On the contrary our model predicts that some proportion of both the genders will not engage in EPM by choice. This is perhaps the first evolutionary model that shows stability of obligate monogamy in spite of the genetic advantages of EPM.

Further, although the model does not incorporate behavioural flexibility and conditional strategies, it is compatible with these concepts. Conditional strategic pluralism [16] can certainly add to the intra-gender differences. The observed intra-gender variation could be genetic, conditional or cultural and currently it is difficult to distinguish between the sources of variation. What our model necessarily demonstrates is that the presence of intra-gender and cross-cultural differences cannot be taken as evidence against the role of genetic and Darwinian forces in shaping human behaviour.

Methods:

The model: The underlying game can be called a “marriage game” in which individuals pair for life but have a choice to desert the partner and pair again. The eight possible strategies considered for the model were

$M^{+}G^{-}P^{-}$

$M^{+}G^{+}P^{-}$

$M^{+}G^{-}P^{+}$

$M^{+}G^{+}P^{+}$

$M^{-}G^{-}P^{-}$

$M^{-}G^{+}P^{-}$

$M^{-}G^{-}P^{+}$

$M^{-}G^{+}P^{+}$

Where M = obligate monogamy, G = individual mate guarding and P = policing and opportunistic blackmailing.

We assumed that the fitness of a strictly monogamous pair was 1. This was taken as the baseline fitness for the model. All polygamous individuals had an additional advantage Z as a result of extra pair mating whereas their partners had to bear a genetic loss L. L could consist of several components including direct genetic loss due to cuckoldry, loss in parenting resources coming from the partner as well as the probability of being deserted and inability to pair again. Individuals actively guarding their mates incurred a cost of guarding gc, and as a result of guarding could reduce their loss L by a fraction S. For guarding to be effective it was necessary to assume $L.S > gc$. We assumed that the cost of policing $pc < gc$ since policing was a cooperative act. The benefit of cooperative mate guarding α, was availed by all individuals alike and was assumed to be directly proportional to the fraction of policing individuals (P^{+}) in the society. Thus the loss L was reduced by a fraction $\alpha.P^{+}$. Reciprocally, for polygamous individuals their benefit Z was reduced by a fraction S when the partner was guarding. As a result of social policing, there was a reduction β in the success of cuckoldry that was directly proportional to P^+. Policing had dual function, as on the one hand it prevented EPM; on the other it exposed adultery. The exposed individuals were assumed to get punishment BB the probability of which was in direct proportion to the fraction of policing individuals in the society. The term BB was taken to include the probability of being exposed and receiving punishment, the direct loss in reproduction owing to deserting by the partner, a bad reputation resulting into reduced probability of pairing again or alternatively the probability of being blackmailed. For a policing individual the opportunities to blackmail were assumed to increase with the number of polygamous individuals in the population. Hence, blackmailing could give direct returns to the policing individuals proportional to the fraction of all polygamous individuals, the proportionality constant being BP. We kept $BP < BB$ throughout the model. A payoff matrix (table 1) was constructed based on these assumptions.

When $Z(1-\beta-S) > BB$, $M^-G^+P^+$ was the only possible ESS. However if $Z(1-\beta-S) < BB$, there was no ESS in the model. Under these conditions a rock-paper-scissor like situation allowed stable or stably oscillating polymorphism. If the population began with $M^+G^-P^-$ as the dominant trait, it could be invaded by any of the polygamous traits owing to the advantage of polygamy, the strongest among the invaders being $M^-G^-P^-$ since it did not pay the cost of guarding and policing. Once polygamy was predominant, guarding and policing became beneficial strategies. Therefore $M^-G^-P^-$ could be invaded by other polygamous traits with guarding and/or policing, the strongest invader being $M^-G^+P^+$. A population of $M^-G^+P^+$ paid a heavy penalty since the probability of punishment and blackmailing was at its maximum. Therefore it could be invaded by $M^+G^+P^+$ if $Z(1-\beta-S) < BB$. This was because a monogamous invader did not encounter punishment and/or blackmailing. Invasion by $M^+G^-P^+$ was also possible if $L.S + Z(1-\beta-S) < BB+gc$.

However this invasion was always weaker than that by $M^-G^+P^+$ due to the difference in the advantage of blackmailing. Once majority of the population was monogamous, the costs of guarding and policing become unnecessary and $M^+G^-P^-$ invaded $M^+G^+P^+$. This completed a rock-paper-scissor like cycle in which at least four players could invade each other cyclically.

Numerical simulations were run for 5000 generations to study the evolutionary dynamics of all the 8 strategies together. As a result of differential fitness advantages at different population composition, all the eight strategies showed stable oscillations when the condition $Z(1-\beta S) < BB$ was satisfied. Oscillations dampened rapidly to give stable steady states with co-existence of typically 4 traits. The most critical parameter for stable or oscillating co-existence and survival of monogamy in particular was blackmailing. The condition $Bp>pc$ was absolutely essential for survival of policing and thereby survival of monogamy. If blackmailing was removed from the model, monogamy did not survive under any set of conditions.

Stable equilibrium in the mono and polygamous traits was possible when *BB* was sufficiently large. With increasing fitness advantage *L* (as well as loss *Z*) due to polygamy, a larger *BB* was required for stability. The line dividing the oscillation and stable steady state areas in figure 4 showed a sudden shift at $LS/gc = Bp/pc$. This was because when LS/gc was smaller, guarding traits did not survive in the population. Therefore a larger *BB* was needed to stabilize polymorphism. When $LS/gc > Bp/pc$, guarding traits replaced non-guarding ones and a lower *BB* was sufficient.

The simulations were run with two sets of assumptions. In the first, no gender difference was assumed and therefore the model was equivalent to assuming that any individual randomly mated with any other. In the second, two genders were assumed and there was random pairing between individuals of opposite genders. Results of the two-gender model were identical to the non-gender model if parameters for both the genders were kept identical. Assuming different cost benefits of EPM for the two genders, we obtained differential outcome for males and females. (The fitness values were relative and gender specific. So that it was not necessary for the model that the average fitness of males and females matched.) Introducing these differences in the model resulted into different proportions of traits in the two genders; nevertheless, polymorphism existed in both the genders. Interestingly satisfying the condition $Z(1-\beta-S) < BB$ in only one of the genders was sufficient for polymorphism in both genders. Difference in L, Z or BB alone or in combination led to substantial gender difference. If males had greater L and Z and/or smaller BB, there was greater proportion of polygamy in males as compared to females. A difference in Bp, on the other hand was unable to induce substantial difference in the proportion of traits across genders.

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Authors' contributions:

MW* and AD developed the model and simulations. BG and AK contributed to conceptual development in the early stages of model.

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Figure legend:

Figure 1 | Rock-Paper-Scissor (R-P-S) like situation.

The pay off matrix shows that there is no particular ESS. Players invade each other cyclically in a complex interplay as indicated by the arrows.

Figure 2 | Oscillating co-existence of all the 8 traits owing to a complex rock-paper-scissor like situation.

Parameters in these simulations were: Loss in genetic advantage due to EPM $L = Z = 0.2$, benefit of social policing availed by all $\alpha = \beta = 0.2$, the cost of policing $pc = 0.01$, cost of mate guarding $gc = 0.02$, punishment $BB = 0.1$, $S = 0.4$ and the probabilistic benefit to the blackmailer $BP = 0.1$.

<u>Colour key:</u>

— $M^+G^-P^-$
— $M^+G^+P^-$
— $M^+G^-P^+$
— $M^+G^+P^+$

— $M^-G^-P^-$
— $M^-G^+P^-$
— $M^-G^-P^+$
— $M^-G^+P^+$

Fig 3 | Damped oscillations giving co-existence of typically 4 traits.

a) Stability was achieved at large *BB* and small *L*. The assumption $Bp>pc$ was most critical for stable polymorphism.

Parameters:

$L = Z = 0.8$, $\alpha = \beta = 0.2$, $pc = 0.0$, $gc = 0.025$, $BB = 0.75$, $S = 0.6$, $BP = 0.1$

b) Making $Bp = 0$ (all other parameters as in **a**) resulted into dominance of a single polygamous and mate guarding trait.

For colour key to figures refer to figure 1.

Fig 4 | Parameter areas for stable and oscillating polymorphism.

Only a single polygamous trait survives at very small values of *BB*. At moderate *BB* there is oscillating coexistence of polygamous and monogamous traits. At higher *BB* there is stable polymorphism. A sudden shift is seen at $LS/gc = Bp/pc$, above which mate guarding traits survive and BB needed for stability is smaller. This is because when $L.S/gc$ is smaller, guarding traits do not survive in population. Therefore a larger *BB* is needed to stabilize polymorphism. When $L.S/gc > BP/ pc$, guarding traits replace the non-guarding ones and a lower *BB* is sufficient. The demarcating boundaries are linear when only guarding or only non-guarding traits are assumed to be present in the simulations.

Legend for boundary colours demarcating areas of stable steady state and oscillating co-existence:

— When both guarding and non-guarding traits are present

— When only guarding traits are present

— When only non-guarding traits are present

— Demarcates the area of polymorphism. Polygamy with or without guarding is an ESS below this line.

Other parameters being $L = Z$, $\alpha = \beta = 0.2$, $pc = 0.01$, $gc = 0.02$, $S = 0.6$, $BP = 0.1$

Fig 5 - Typical results of the gender difference model.

When parameters were different for the two genders, polymorphism resulted in both genders but the predominant traits were different. Interestingly satisfying the condition $Z.(1-\beta-S) < BB$ in only one of the genders was sufficient for polymorphism in both genders. Increased model complexity frequently led to complex waves or chaos, nevertheless a few traits remained consistently dominant in each gender.

a) Female traits

$L = Z = 0.15$, $\alpha = \beta = 0.3$, $pc = 0.01$, $gc = 0.018$, $BB = 0.1$, $S = 0.4$, $BP = 0.1$

b) Male traits

$L = Z = 0.2$, $\alpha = \beta = 0.3$, $pc = 0.01$, $gc = 0.018$, $BB = 0.09$, $S = 0.4$, $BP = 0.1$

For colour key to figures refer to figure 1.

Table 1: The payoff matrix

Population Invader	$M^+G^-P^-$	$M^+G^+P^-$	$M^+G^-P^+$	$M^+G^+P^+$	$M^-G^-P^-$	$M^-G^+P^-$	$M^-G^-P^+$	$M^-G^+P^+$
$M^+G^-P^-$	1	1	1	1	$1-L$	$1-(L(1-\alpha))$	$1-L$	$1-(L(1-\alpha))$
$M^+G^+P^-$	$1-pc$	$1-pc$	$1-pc$	$1-pc$	$1-L-pc+BP$	$1-(L(1-\alpha))-pc+BP$	$1-L-pc+BP$	$1-(L(1-\alpha))-pc+BP$
$M^+G^-P^+$	$1-gc$	$1-gc$	$1-gc$	$1-gc$	$1-(L(1-S))-gc$	$1-(L(1-\alpha-S))-gc$	$1-(L(1-S))-gc$	$1-(L(1-\alpha-S))-gc$
$M^+G^+P^+$	$1-gc-pc$	$1-gc-pc$	$1-gc-pc$	$1-gc-pc$	$1-(L(1-S))-gc-pc+BP$	$1-(L(1-\alpha-S))-gc-pc+BP$	$1-(L(1-S))-gc-pc+BP$	$1-(L(1-\alpha-S))-gc-pc+BP$
$M^-G^-P^-$	$1+Z$	$1+(Z(1-\beta))-BB$	$1+(Z(1-S))$	$1+(Z(1-\beta-S))-BB$	$1+Z-L$	$1+(Z(1-\beta))-(L(1-\alpha))-BB$	$1+(Z(1-S))-L$	$1+(Z(1-\beta-S))-(L(1-\alpha))-BB$
$M^-G^+P^-$	$1+Z-pc$	$1+(Z(1-\beta))-pc-BB$	$1+(Z(1-S))-pc$	$1+(Z(1-\beta-S))-pc-BB$	$1+Z-L-pc+BP$	$1+(Z(1-\beta))-(L(1-\alpha))-pc-BB+BP$	$1+(Z(1-S))-L-pc+BP$	$1+(Z(1-\beta-S))-(L(1-\alpha))-pc-BB+BP$
$M^-G^-P^+$	$1+Z-gc$	$1+(Z(1-\beta))-gc-BB$	$1+(Z(1-S))-gc$	$1+(Z(1-\beta-S))-gc-BB$	$1+Z-(L(1-S))-gc$	$1+(Z(1-\beta))-(L(1-\alpha-S))-gc-BB$	$1+(Z(1-S))-(L(1-S))-gc$	$1+(Z(1-\beta-S))-(L(1-\alpha-S))-gc-BB$
$M^-G^+P^+$	$1+Z-gc-pc$	$1+(Z(1-\beta))-gc-pc-BB$	$1+(Z(1-S))-gc-pc$	$1+(Z(1-\beta-S))-gc-pc-BB$	$1+Z-(L(1-S))-gc-pc+BP$	$1+(Z(1-\beta))-(L(1-\alpha-S))-gc-pc-BB+BP$	$1+(Z(1-S))-(L(1-S))-gc-pc+BP$	$1+(Z(1-\beta-S))-(L(1-\alpha-S))-gc-pc-BB+BP$

Fig. 1

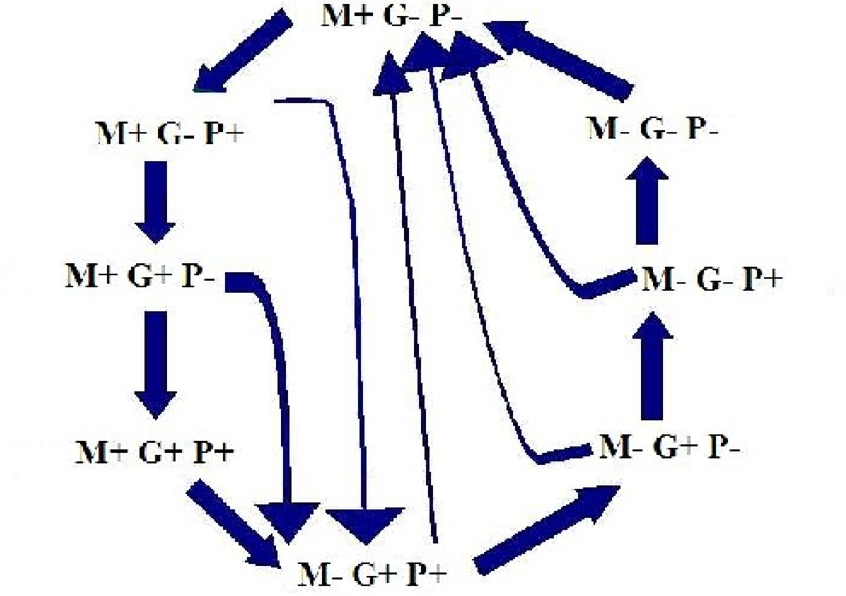


Fig. 2

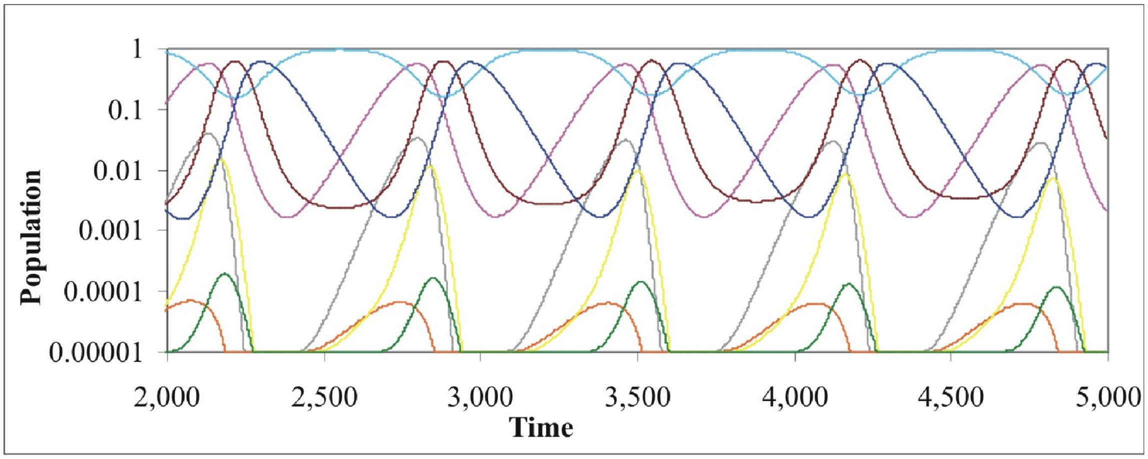

1
0.1
0.01
0.001
0.0001
0.00001
Population
2,000
2,500
3,000
3,500
4,000
4,500
5,000
Time

Fig. 3 A

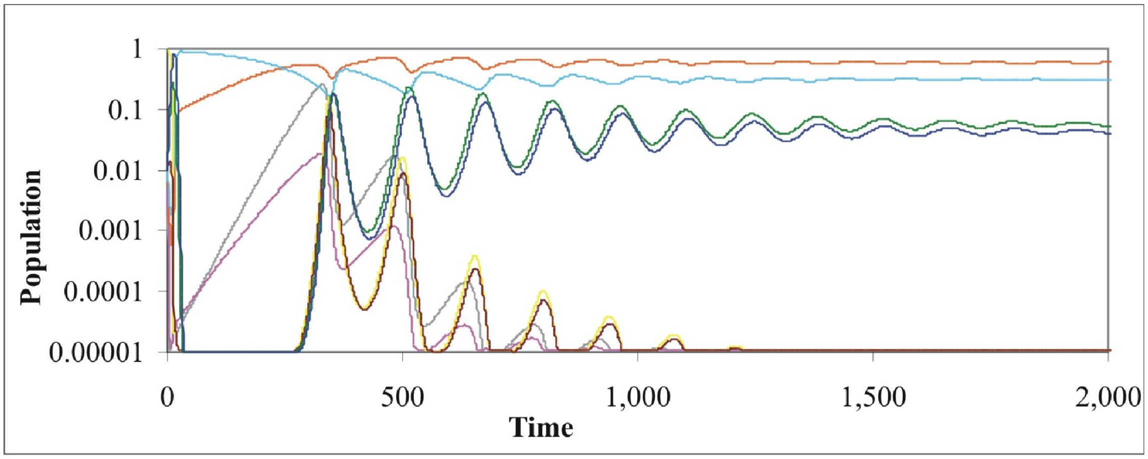

1
0.1
0.01
0.001
0.0001
0.00001
Population
0
500
1,000
1,500
2,000
Time

Fig. 3 B

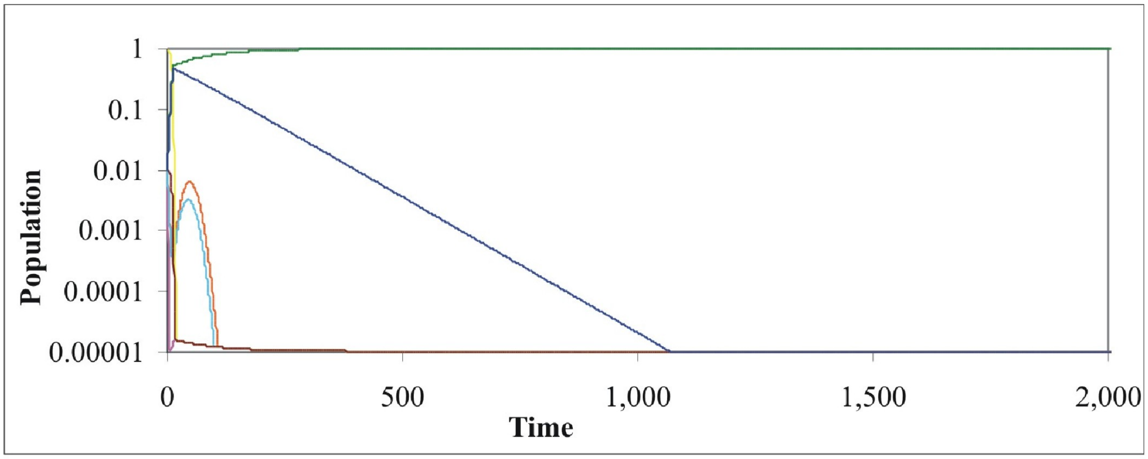

Population
1
0.1
0.01
0.001
0.0001
0.00001
0
500
1,000
1,500
2,000
Time

Fig. 4

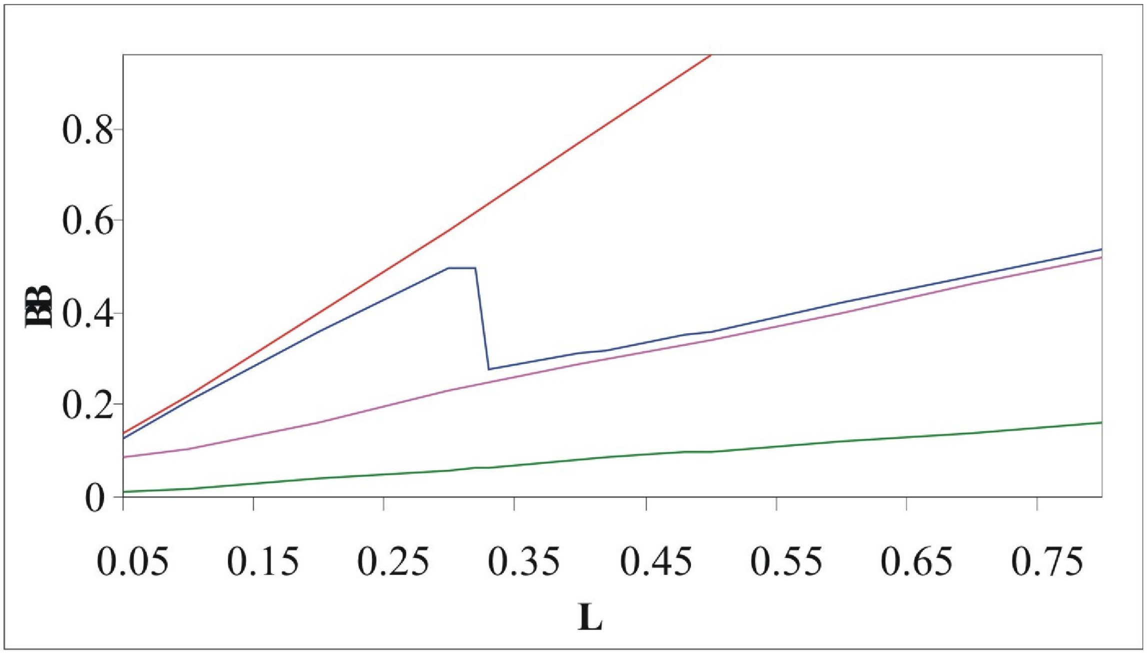

BB
0.8
0.6
0.4
0.2
0
0.05
0.15
0.25
0.35
0.45
0.55
0.65
0.75
L

Fig. 5 A

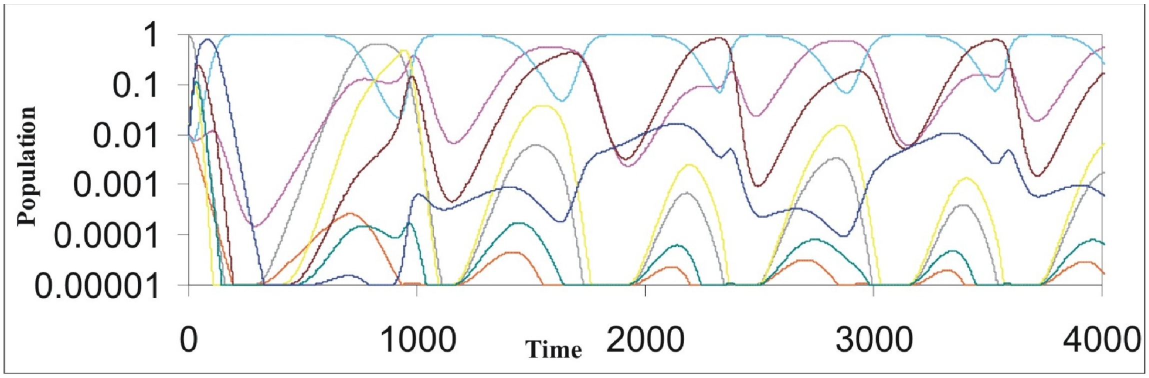
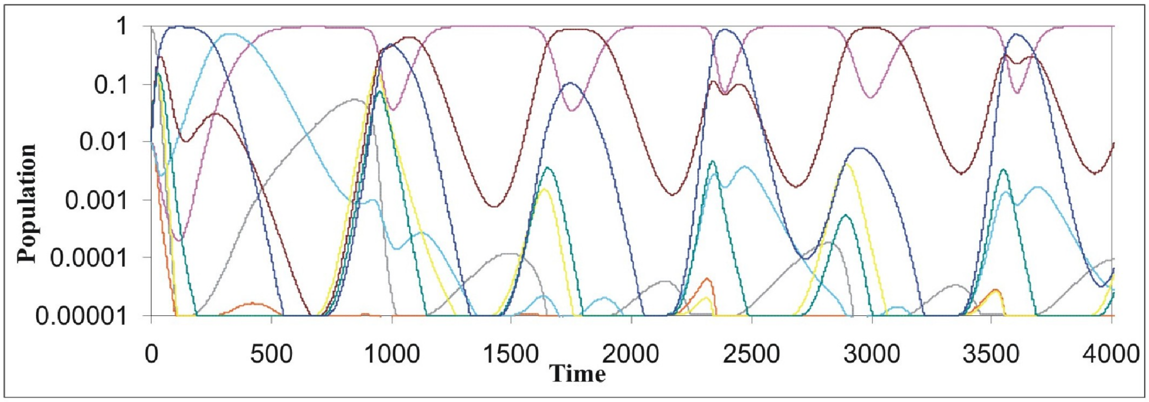

1
0.1
0.01
0.001
0.0001
0.00001
Population
0
1000
2000
3000
4000
Time

Fig. 5 B


1
0.1
0.01
0.001
0.0001
0.00001
Population
0
500
1000
1500
2000
2500
3000
3500
4000
Time