Evolutionary Game Theory
HUL311: Term Paper

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The term paper is divided into two parts. The first part is an overview of concepts of evolutionary game theory with some examples. The second part focuses on evolutionary analysis of the Red Queen and the Red King effects, and some relevant examples. In hostile relationships (prey/predator, host/parasite), faster evolution is beneficial for species for coexistence, which is the Red Queen effect. In some other scenarios, specifically mutualisms, slow evolution is better in the long run to uphold the beneficial relationship, which is the Red King effect.

Contents

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1 Introduction

What we have studied in (non-cooperative) game theory is that equilibrium is justified in terms of rationality, common knowledge of the game and its aspects like preferences and player choices. Evolutionary game theory dispenses all three of these assumptions and studies iterations of the game where the beliefs of the players might change, which can potentially give rise to newer dynamics in the system. One of the crucial assumptions of game theory is each player being rational, which need not be the case in evolutionary game theory. A player may start with a sub-optimal belief and over the iterations, learn from the outcomes and update his/her beliefs.
McKenzie [2002] in his article describes two broad approaches to Evolutionary Game Theory. The first approach is used to find the set of evolutionary stable strategies, while the other approach is to study the evolution of system over time.

1.1 Conceptual Overview

1.1.1 Evolutionarily Stable Strategy

Evolutionarily stable strategy (ESS) is a strategy which when adopted by a population of different species becomes resistant to invasion by foreign strategies granted a sufficiently small and positive invasion barrier, that is, the strategy is robust to natural selection.
The set of pure strategies is denoted by $K = 1, 2, ..., k$ and the associated mixed strategy set is $\Delta = x \in R^k_+ : \sum_{i \in K} x_i = 1$. The set of best replies $x \in \Delta$ to $y \in \Delta$ is $\beta^*(y) \subset \Delta$, and $u(x, y)$ is the payoff function. The payoff is defined as reproductive value or fitness in biological context. In the anthropological/economic context, a participant employing ESS is better off than the one employing alternate strategy in interactions.

Definition 1. *A strategy $x \in \Delta$ is said to be evolutionarily stable if for every mutant strategy $y \neq x$, there exists some $\bar{\epsilon} \in (0, 1)$ such that the below inequality holds for every $\epsilon \in (0, \bar{\epsilon})$ [Smith and Price [1973]].*

$$u(x, \epsilon y + (1 - \epsilon)x) > u(y, \epsilon y + (1 - \epsilon)x) \tag{1}$$

Assumptions in the defined context:

1. The population in which game is played is large.
2. There is one mutation at a time.
3. The population adjusts to status quo before any mutation.

Like in NE, evolutionary game theory does not explain how the state is arrived at, rather it evaluates whether a strategy is evolutionarily stable, given the game.

Proposition 1. *Evolutionary stable strategies are a subset of Nash equilibria strategies.*

$$\Delta^{ESS} = \{x \subset \Delta^{NE} : u(y, y) < u(x, y) \forall y \in \beta^*(x), y \neq x\} \tag{2}$$

It follows that if (x, x) is a strict Nash equilibrium, then x is evolutionarily stable and there exist no alternative best replies. Thus evolutionary stability does not in general imply that average population fitness $u(x, x)$ is maximized. The set of ESS is finite (possibly empty).

Proposition 2. *If $x \in \Delta^{ESS}$ and $C(y) \subset C(x)$, ($C(.)$ is the set of support strategies), for some strategy $y \neq x$, then $y \notin \Delta^{NE}$ [Haigh [1975]].*

Proposition 3. *If $x \in \Delta$ is weakly dominated, then $x \notin \Delta^{ESS}$.*

Proposition 4. *$x \in \Delta^{ESS}$ if and only if x has a uniform invasion barrier.*

1.1.2 Replicator Dynamics

An evolutionary process combines mutation and selection processes. The mutation process brings the variety in the population, while the selection process ensures survival of the fittest in the population. The replicator model helps us to understand the evolution of different species over time. The underlying assumptions are:

1. The population consists of different kinds of species, all of which follow a different pure strategy.

2. The off-springs follow the strategy which their parent follows without any error.

3. The rate of reproduction of a species depends on the proportion of that species and the fitness of the species.

If $e^1, ..., e^k \in S$ are the pure strategies available to a player, then that player's strategy will be denoted by the column vector $\vec{x}$. The i^{th} component of $\vec{x}$ gives the probability of playing strategy e^i. Playing a pure strategy e^j is represented by the vector whose j^{th} component is 1, and all other components are 0. When the payoff for a player is specified by a payoff matrix A, a player using strategy $\vec{x}$ against an opponent with strategy $\vec{y}$ will have payoff $\vec{x}^T A\vec{y}$, and average fitness of the population is $\vec{x}^T A\vec{x}$.
Let t denote time. There are k different pure strategies which a player can play, so the maximum number of different species which can be accommodated in the model is k and the length of vector $\boldsymbol{x}(t)$ is k. Let $\boldsymbol{e^j}$ denote the j^{th} pure strategy which is played by x_j and $u(\boldsymbol{e^j}, \boldsymbol{x})$ denote the expected payoff of playing the j^{th} pure strategy in population $\boldsymbol{x}$ and as defined in equation 3.

$$u(\boldsymbol{e^j}, \boldsymbol{x}) = \sum_{i=1}^{i=k} x_i u(\boldsymbol{e^j}, \boldsymbol{e^i}) \tag{3}$$

Let the population average payoff, $u(\boldsymbol{x}, \boldsymbol{x})$ be defined as,

$$u(\boldsymbol{x}, \boldsymbol{x}) = \sum_{j=1}^{j=k} x_j u(\boldsymbol{e^j}, \boldsymbol{x}) \tag{4}$$

The replicator model, which is defined by a set of differential equations giving the growth rate of different species is given by

$$\dot{x_j} = x_j[u(\boldsymbol{e^j}, \boldsymbol{x}) - u(\boldsymbol{x}, \boldsymbol{x})] \quad \forall j \in \{1, 2, ..., k\} \tag{5}$$

Proposition 5. *ξ denotes the solution mapping for the replicator dynamics, and $\xi(t, x^o) \in \Delta$ is the population state at time $t \in R$ if the initial state is $x^o \in \Delta$. If a pure strategy i is strictly dominated, then $\xi_i(t, x^o)_{t\to\infty} \to 0$ for any $x^o \in int(\Delta)$.*
This means that the replicator dynamics wipes out all strictly dominated pure strategies from the population, granted all pure strategies in the game are initially present.

1.2 Examples

1.2.1 Snowdrift/Chicken/Hawk-Dove

This is a contest over a shareable resource. The contestants can be either Hawk or Dove [Smith and Price [1973]]. These are two subtypes or morphs of one species with different strategies. The Hawk first displays aggression, then escalates into a fight until it either wins or is injured (loses). The Dove first displays aggression, but if faced with major escalation runs for safety, that is, yields. If not faced with such escalation, the Dove attempts to share the resource. Resource is given the value V, damage from losing a fight is given cost C.

	Hawk	Dove
Hawk	$\frac{1}{2}(V-C)$	V
Dove	0	V/2

Table 1: Payoff Matrix for row player in the Hawk-Dove game

Given that the cost of a fight exceeds the value of a victory: $v < c$, pure strategy 2 (yield) is the unique best reply to strategy 1 (fight), and vice versa. Each of the asymmetric pure-strategy pairs $(1, 2)$ and $(2, 1)$, respectively, constitutes a strict Nash equilibrium. There is also a symmetric Nash equilibrium in mixed strategies. If player 2 plays strategy I with probability $l = v/c$, then player l's two pure strategies yield the same expected payoff. Therefore the mixed-strategy pair (x, x), where x assigns probability l to strategy 1 and $1 - l$ to strategy 2, constitutes a Nash equilibrium.
Consider $v = 4$ and $c = 6$. Unique symmetric NE is $x = (\frac{2}{3}, \frac{1}{3})$. For $x, y \in \Delta : u(x-y, y) = (x_1 - y_1)(2 - 3y_1) = \frac{1}{3}(2 - 3y_1^2)$, which is > 0 except when $y = x$, and thus $x \in \Delta^{ESS}$. Evolutionary stability rejects pure hawkishness and pure doveness. Replicator dynamics is

$$\dot{x_1} = (2 - 3x_1)(1 - x_1)x_1$$

As C becomes smaller than V, the mixed strategy equilibrium moves to the pure strategy equilibrium of both players playing hawk (Hawk–Dove transforming into Prisoner's Dilemma).

1.2.2 Prisoner's Dilemma

The standard game of Prisoner's Dilemma, an example of which is given in Table 2, has a Nash Equilibrium strategy of (Defect, Defect). We observe that this Nash Equilibrium is a sub-optimal whereas (Cooperate, Cooperate) is the optimal strategy for the game. (Defect) is the unique best reply to any strategy and hence, the unique ESS of the game. Evolutionary selection, as modeled by the ESS criterion, does not support any degree of "cooperation" in the one-shot Prisoner's Dilemma Game.

	Defect	Cooperate
Defect	(-10,-10)	(0,-20)
Cooperate	(-20,0)	(-1,-1)

Table 2: Payoff matrix for Prisoner's Dilemma

A matrix is $\begin{pmatrix} -1 & -20 \\ 0 & -10 \end{pmatrix}$, then the average fitness of population is $\vec{x}^T A \vec{x} = 9x^2 - 10$. The replicator dynamics for the cooperators (first component of $\vec{x}$) is

$$\dot{x_1} = x(A\vec{x})_1 - \vec{x}^T A \vec{x} = x_1(19x_1 - 20 - 9x_1^2 + 10) = -x_1(9x_1 - 10)(x_1 - 1)$$

We observe in Figure 1 that $\forall x \in (0, 1)$, $\dot{x} < 0$, which means that frequency of cooperation is strictly decreasing. Analysis of the iterated prisoner's dilemma using this representation and the replicator dynamics leads to coupled nonlinear differential equations. The analysis, while tedious, is not very informative, populations do not converge to a fixed point and there is no known optimal strategy for the repeated game [Hofbauer and Sigmund [1998]].

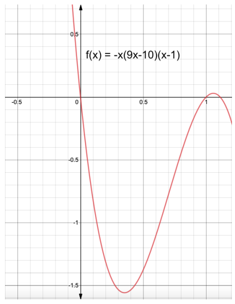
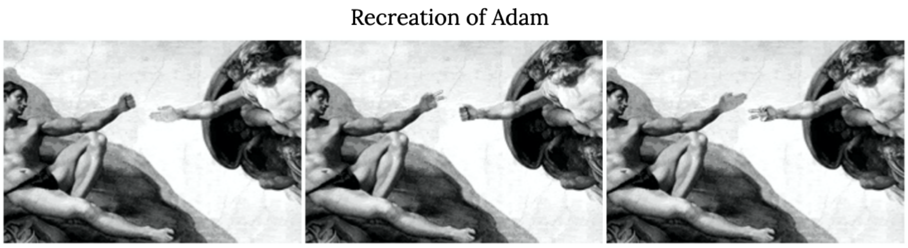


Figure 1: Prisoners Dilemma Cooperator dx/dt

More possible variations are multiple players, asymmetry in the game, and asynchronous moves, and signalling.

1.2.3 Rock-Paper-Scissors



The game of Rock Paper Scissors has 3 strategies such that Rock beats Scissors, Scissors beats Paper and Paper beats Rock. There is no pure strategy NE. The mixed strategy NE is when each player plays each of the 3 actions with equal probability, 1/3.
Why no player would deviate from the NE is unclear, as even though there is no gain in doing so, there is no harm either. But it is observed that the deviants win/lose less frequently than the non deviants, and draw more often. So whether a strategy is evolutionarily stable or not depends on the payoffs assigned to winning and losing relative to drawing.

	Rock	Paper	Scissors
Rock	1,1	0,a	a,0
Paper	a,0	1,1	0,a
Scissors	0,a	a,0	1,1

Table 3: Payoff matrix for Rock-Paper-Scissor

When $a > 2$, incentive of winning is higher than payoff of drawing, whereas, when $a < 2$, incentive of winning is lower than drawing. For $a > 1$, there exists a mixed NE where each individual independently randomizes between the 3 actions with equal probability. For $a > 2$, NE is evolutionary stable, whereas for $a < 2$ it is not.
The replicator dynamics for generalised game is (similar for x_2 and x_3)

$$\dot{x_1} = (x_1 + ax_2 - xAx)x_1$$

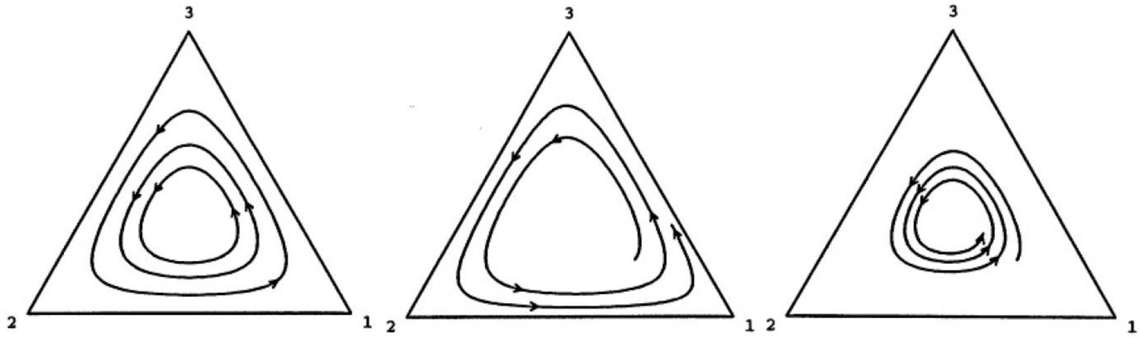


Figure 2: Replicator Dynamics for the game when a) $a = 2$, b) $a < 2$ and c) $a > 2$

For any initial state $x^o \in int(\Delta)$, the solution moves perpetually along the closed curve on which $x_1 x_2 x_3 = x_1^o x_2^o x_3^o = \gamma$. Interior solution trajectories to the replicator dynamics are periodic when $a = 0$. In contrast, if $a < 2$, then the dynamic paths induced to move outward, toward hyperbolas with lower γ from all interior initial states except $x_o = (1/3, 1/3, 1/3)$ Hence $(1/3, 1/3, 1/3)$ is evolutionarily stable when $a > 2$, neutrally but not evolutionarily stable when $a = 2$, and not even neutrally stable when $a < 2$. Conversely, If $a > 2$, then all trajectories move inward, toward hyperbolas with higher γ. Hence, for any $a > 2$, the unique Nash equilibrium strategy in this game is asymptotically stable and attracts the whole interior of the state space.

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2 Problems in Evolutionary Game Theory

The strategies that we have discussed in game theory require rational players to be able to understand the opponents' moves and iterate over possible interactions to arrive at a best response. What intrigued us is that in biological, social and cultural interactions, players intentionally and not also exercise speed as a strategy, wherein intuitively being fast is advantageous, but as old wisdom suggests, slow has better payoffs based on scenario too. In order to address this problem of exercising speed of evolution as a strategy without any rational preemption, we did some reading and stumbled upon the Red Queen and King effect.

2.1 Red Queen Effect

Now, here, you see, it takes all the running you can do, to keep in the same place.

Theorised by Van Valen [1973], who drew lessons from Lewis Carroll's 'Through The Looking Glass' to explain the constant (age independent) extinction probability as observed in the paleontological record caused by co-evolution between competing species.

Definition 2. ***Law of Constant Extinction***: *the probability of extinction for species and larger evolutionary groups bears no relation to how long it may have already existed.*

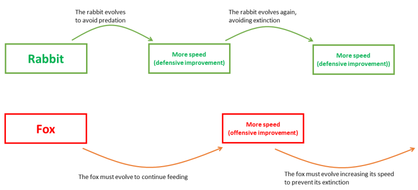

Figure 3: Rabbit evolves to escape the fox, and the fox evolves to reach the rabbit. Evolution is constant, if one of the two stops evolving, it perishes [red [2020]].

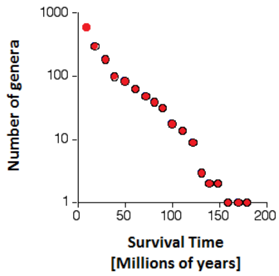

Figure 4: Linear relationship between survival times and the log number of genera suggests that probability of extinction is constant over time [red [2020]].

Van Valen used The Red Queen analogy to highlight the fact that species must evolve continuously as pitted against its natural competitors, or perish.
Marrow et al. [1992] gave a mathematical formulation of Red Queen model as an evolutionary game between a predator and a prey in terms of coevolution. Rosenweig et al. [1987] put this problem in a different perspective by defining Red Queen in terms of ESS to find coevolution rates. Both of these respective formulations have been discussed henceforth.

- Marrow et al. [1992]
  For simplicity, it is assumed that one trait, say body size, undergoes evolution in each species (1 subscript represents prey and 2 predator), denoted by s_1 and s_2. Corresponding to each point in the phenotype space is a phase space, this being the space of population densities, x_1 and x_2. This is adopting the Lotka-Voltera model

$$\dot{x_1} = x_1 f(x_1) = x_1(r_1 + \alpha x_1 + \beta x_2)$$

$$\dot{x_2} = x_2 f(x_2) = x_2(r_2 + \gamma x_1)$$

  $s_1, s_2, x_1, x_2, r_1, r_2 > 0,\ \alpha < 0$
  Parameters $r1$ and $r2$ are the per capita rates of increase at low density. α is a self limitation term in preys. β represents effect of the predator on per capita rate of increase of prey (similar logic for γ), and intuitively, $\beta < 0$ and $\gamma < 0$. The model proceeds to make assumption about the form of α, β and γ. The choice of model gives equilibrium density $\hat{x_1}$, $\hat{x_2}$ as the solution of (11) and (7).

$$f_1 = r_1 + \alpha(s_1)\hat{x_1} + \beta(s_1, s_2)\hat{x_2} = 0 \tag{6}$$

$$f_2 = r_2 + \gamma(s_1, s_2)\hat{x_1} = 0 \tag{7}$$

  The equilibrium is thus at $\hat{\boldsymbol{x}} = (\hat{x_1}, 0, \hat{x_2}, 0)$. If the equation has no solution, then prey and predator cannot coexist for the given values of body sizes (whatever trait). If mutations are represented as perturbations changing body size to $s_1 + \epsilon_1$ and $s_2 + \epsilon_2$, then capita rates of increase of the mutants should be greater than those of their predecessors at $\hat{\boldsymbol{x}}$, that is,

$$f_1' = r_1 + \alpha_{s_1+\epsilon_1}\hat{x_1} + \beta_{s_1+\epsilon_1, s_2}\hat{x_2} > 0$$

$$f_2' = r_2 + \gamma_{s_1, s_2+\epsilon_2}\hat{x_1} > 0$$

  Detailed simulation with assumed values of parameters is presented in the paper, and we have shared some examples.

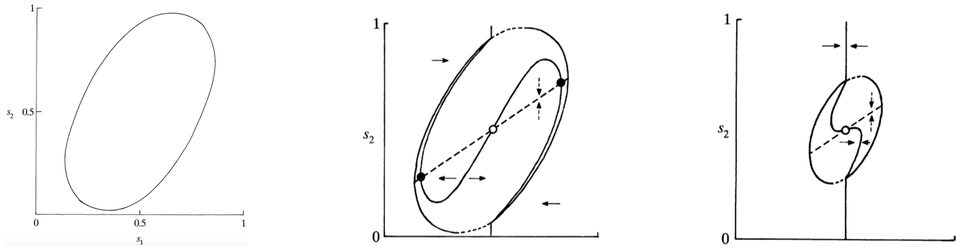

Figure 5: First is phenotype space of prey and predator body size, (s_1 and s_2). Inside the oval, predator coexists with prey; on and outside the oval line, predator density zero at equilibrium. Broken lines show where prey evolution would lead to predator extinction. Solid arrows show change in body size caused by fixation of successfully invading mutants in prey, and broken arrows show that for predator. Solid/broken line in oval is line of zero selection. Evolutionary saddle is o and ESS is • In the second figure, parameter values are tuned to get 2 ESS, 1 saddle, and third figure has one saddle only [Marrow et al. [1992]].

- Rosenweig et al. [1987]
  Every individual has a collection of phenotypes, say $(u_1, u_2, u_3 \dots)$, and i^{th} combina-

tion of traits is given by $(u_{1i}, u_{2i}, u_{3i} \dots)$ abbreviated by u_i. Let there be m such combinations, $u = u_1, u_2, u_3 \dots, u_m$. Let them occur with frequency $(p_{u_1}, p_{u_2}, \dots, p_{u_m}) = p_u$ in the population of density N_u. If two more sepcies v and w are added to the model, then the fitness generating function for individual with phenotype ϕ_j, where j is the species, is

$$G_j(\phi_j, u, v, w, p_u, p_v, p_w, N) \tag{8}$$

The rate of evolution (similarly for v and w) is given by

$$\Delta u_i = a_u \frac{\partial G_u(.)}{\partial \phi_{ui}},\ a_u > 0 \tag{9}$$

Using (8) and (9), custom inputs can be given to evaluate Red Queen emergence and the ESS, as has been done in the paper. Below we present two results relevant to the discussion.

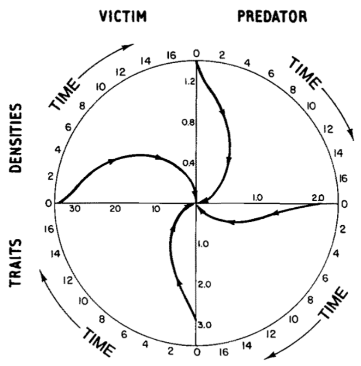

Figure 6: Choice of two traits- running speed and metabolic constant (prey)/searching ability (predator), sum of trait values is constant (correlated and constrained, tradeoff on each choice). Each parameter's trajectory is plotted in one-quarter of polar coordinate space. Angle is time, and radius is parameter minus its ESS value. Values converge on the ESS [Rosenweig et al. [1987]].

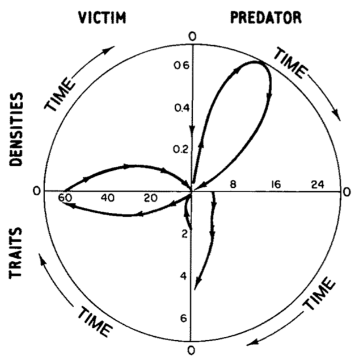

Figure 7: Here, extreme best is possible, i.e., sum of trait values is not constrained and is allowed to grow. Red Queen evolution in a predator and victim. Equilibrium densities of both species converge on evolutionarily stable values (the center). The trait values keep growing, diverging from the center, keeping a constant ratio between them after the densities reach the center [Rosenweig et al. [1987]].

2.1.1 Biological interpretation

Extensively discussed in Bell [1982], a species chooses to mate with the opposite sex by looking at desirable traits that it would want in its offspring. Sexual organisms must spend resources to find mates. In the case of sexual dimorphism, usually one of the sexes contributes more to the survival of their offspring (usually the mother). In such cases, the only adaptive benefit of having a second sex is the possibility of sexual selection, by which organisms can improve their genotype. These would aid the offspring to survive in an environment that requires it to be fit, thus speeding up evolution with a desirable trait passing down the evolutionary chain, making them immune to falling prey to any other species.
The primary assumption of the Red Queen hypothesis is that parasites that are able to infect common host genotypes achieve a significant selective advantage, which thus favors rare hosts. The theory of negative frequency-dependent selection by parasites predicts that loci

involved in host infectivity should be polymorphic both within and between natural populations and that genotypic combinations of alleles at these loci should oscillate in frequency over time as local parasites continually adapt to their host population. Rare host genotypes escape infection and increase in frequency. This advantage drives continual oscillations through time in the frequency of host genotypes and their matching parasite genotypes. Coevolution as depicted in Figure 8 is proposed to maintain genetic diversity in host and parasite populations. Host genotypes decline when common and increase when rare due to negative frequency-dependent selection exerted by the coevolving parasite population. The time-lag in the parasite genotype frequency reflects the period required for the parasite population to adapt to the changing host population.

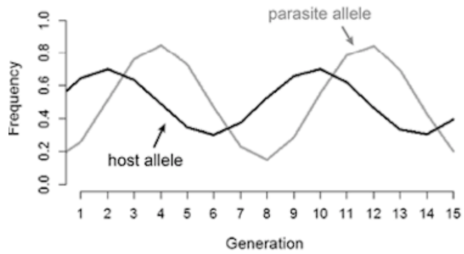

Figure 8: Oscillations through time in the frequency of a host genotype (black) and its matching parasite genotype (gray)

2.1.2 Social perspective

In this section we present three different scenarios which can be modelled with Red Queen Theory.

1. Climate Change: Let the accelerating climate change be the Red Queen and the man be Alice from the book. The man, however hard he tries is not able to reduce carbon emissions against the accelerating climate change, just like, Alice was unable to keep up with the Red Queen. Treaties like Paris Agreement might help us to reduce emissions but even so we might end up just at the beginning, just like Alice, who ran but was always in the same place. What we need is to reduce out dependence on conventional resources at such a scale at which we are able to outrun the acceleration of climate change [Porter [2019]].

2. Pharmaceutical Industries: All kinds of companies invest heavily in their research and development program to provide better goods and services to consumers, but pharmaceutical companies invest the highest among all. Going along with the analogy of Red Queen, we can consider different firms to be different species. One firm finds a new method to manufacture a previously expensive drug cheaply. This firm will be able to sell the drug at more competitive price than its competitors, and thus its market share will increase. Soon, the rival companies will try to copy the same manufacturing process and they all will be able to make the same drug at reduced cost. Thus the initial advantage which the first firm had, has now been gone and all firms are back at same level. This is very similar to a species developing a body trait, which can help it in its survival. This feature will help it for some time, but after that all the other species will develop some or the other feature and all the species will come at equal footing.

3. Arms-Race: Consider two neighbouring countries who are at the verge of a war between them. Both have a decision to make on whether or not additional army should

deployed at the common border. Table 4 gives the respective payoffs for both the countries. If both countries decide against deploying an additional army, both save on money as well as on territory. If both countries decide to deploy the army, money is spent on mobilising the force, whereas the territory of each country is saved. The last case is when one country decides to mobilise the army, while other does not. In this case, the one with the extra army wins some land, which the country values higher than the money spent on mobilising the extra force. The payoff matrix resembles the structure of Prisoner's Dilemma. In this game, even if one country outwits the other in mobilising the army, its victory will be short lived as then the other country will also mobilise the reserve force. Thus, this might keep going, with each country adding extra security personals at the border thus evolving in a way but the other country keeps following with its own evolution, thus no actual benefit is received by any country even after evolution.

	Deploy	Not Deploy
Deploy	(3,3)	(15,0)
Not Deploy	(0,15)	(10,10)

Table 4: Payoff matrix for Arms Race

2.2 Red King Effect

2.2.1 Introduction

So when does the tortoise defeat the hare to win the race?

Mutualism, the phenomenon in which two species are dependent on each other for a particular resource, provide benefits to those who participate in them. A question that follows this definition, is that of allocation of benefits. As a mutualism evolves, how will these benefits come to be allocated among the participants? Role of evolutionary rates in the establishment of mutualism and the partitioning of benefits among mutualist partners is analysed. Slowly evolving species is likely to gain a disproportionate share of benefits. This is termed as Red King Effect. A Red King effect occurs when a speed differential between evolving populations makes it more likely that the evolutionary dynamics carry those populations to an outcome that advantages the slow population [O'Connor [2017]].

	Generous	Selfish
Selfish	(2,1)	(0,0)
Generous	(k,k)	(1,2)

Table 5: Payoff matrix for Mutualistic Interations

Consider the payoff matrix for Mutualistic Interaction. If both players make selfish offers, the association breaks down and the players fail to generate the benefits that result from mutualism. If one makes a generous offer and the other makes a selfish offer, the selfish player gets 2 units and the generous players gets 1. If both players make generous offers, each gets an amount k of the benefits. In mutualism, participants come from two populations of species to engage in pairwise interactions.
The replicator dynamics for role-asymmetric games for two populations with evolutionary

rates m and n, respectively, where x is the frequency of selfish players in the species 2, and y is the frequency of selfish players in the species 1 population is

$$\dot{x} = mx(2(1-y) - (2(1-y)x + (y + k(1-y))(1-x))) \tag{10}$$

$$\dot{y} = ny(2(1-x) - (2(1-x)y + (x + k(1-x))(1-y))) \tag{11}$$

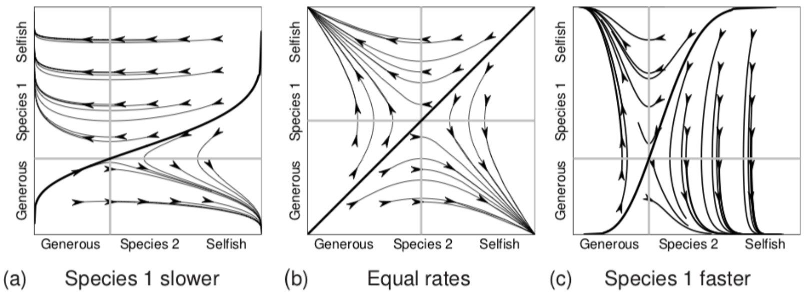

Figure 9: The effect of evolutionary rate on domains of attraction when k = 1.5. (Left) Species 1 evolves eight times slower than species 2. (Center) Equal rates of evolution. (Right) Species 2 evolves eight times slower. In this game, the slower-evolving species has the larger domain of attraction around its favored equilibrium [Bergstrom and Lachmann [2003]]

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Depending on the payoffs, changes in shape of the separatrix can increase the domain of attraction around the equilibrium favoring the slower species or the one favoring the faster species. Figure 9 shows the evolutionary trajectories for the game in which k = 1.5. The domain of attraction around the upper left equilibrium increases in size as the relative rate of evolution by species 1 decreases. That is, the slower that species 1 evolves, the higher chance it has of reaching its favored equilibrium. This is the Red King effect.

2.2.2 Biological interpretation

The paper on Red King effect by Bergstrom and Lachmann [2003] showed the relation between evolutionary rates and fitness of a species in a population consisting of only two species. Shibasaki [2018] discusses whether Red King effect also holds in a population of more than two different interacting species. Let table 5 denote the payoffs each individual receive when two individuals from different species meet of them meet. We add a constraint on the value of k, $0 < k < 2$.

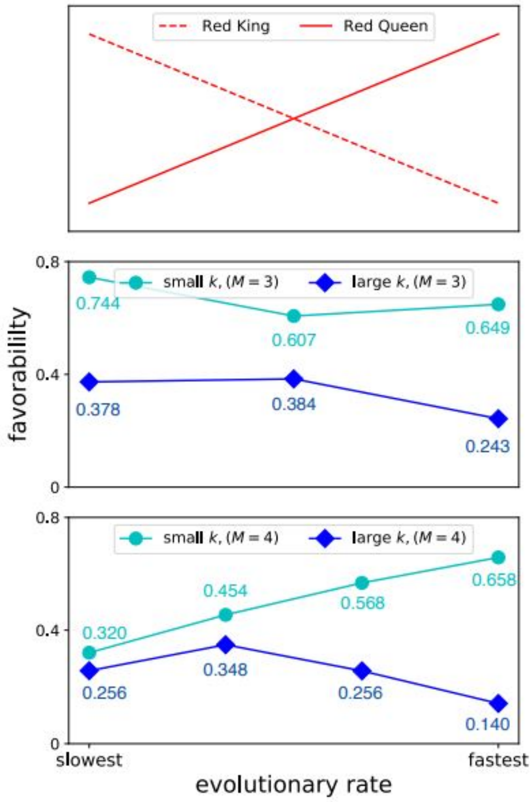


Figure 10: The topmost figure shows the ideal Red King and Red Queen effects. The middle picture shows the favorability for a population of 3 species. $r = (1/8, 1, 8)$, small k = 0.5 and large k = 1.5. The bottom-most picture shows the same for a population of 4 species. $r = (1/8, 1/2, 2, 8)$, small k = 0.5 and large k = 1.6. [Shibasaki [2018]]

Let there be M different species in the population and let x_i denote the proportion of generous individuals in i^{th} species. Let r_i be the evolutionary rate, f_i^g be the mean fitness of generous individuals and $\bar{f}_i$ be the mean fitness of species i. The replicator dynamics is given by equation 12

$$\dot{x_i} = r_i x_i (f_i^g - \bar{f}_i) \tag{12}$$

The paper makes an assumption that the population of each species is infinitely large. This leads to an easier replicator dynamics equation, which is given by equation 13.

$$\dot{x_i} = r_i x_i (1 - x_i)\{1 + (k - 3)\bar{x}_{j \neq i}\} \tag{13}$$

where $\bar{x}_{j \neq i}$ represents the average fraction of individuals except species i.
Figure 10 shows the favorability of a species to evolve selfishly at stable equilibrium. The simulations are run for a large number of times and the probabilities are averaged out with initial distribution of generous individuals within each species drawn from a random distribution.
We observe that unlike in the original paper by Bergstrom and Lachmann, where we had a clear relationship between evolutionary rates and favorability, we find it difficult to observe such in case of multi-species population. This might be attributed to the fact that in two-species population, the stable equilibrium had one clear winner (the selfish species) and one loser, but in multi-species population the payoff of different species becomes highly dependent on k. For example there exists a stable equilibrium in the 3 species model with

1 generous and 2 selfish species, and if $0 \leq k < 1$, then the payoff received by each species is 2. This shows that 2 selfish species do not win against the generous species.

2.2.3 Social perspective

As an example of social perspective of Red King, we evaluate as to why a minority group is discriminated against in situations of bargaining or resource division [O'Connor [2017]]. Consider the Nash demand game between two players belonging to different groups of society, minority and majority. Say a resource of size 10 is being divided. Medium demand is 5, which is an even split of resources. Low and High demands can take any values such that $L + H = 10$, and $L < 5 < H$, like 2 and 8, or 4 and 6.

	Low	Medium	High
Low	(L, L)	(L, 5)	(L, H)
Medium	(5, L)	(5, 5)	(0, 0)
High	(H, L)	(0, 0)	(0, 0)

Table 6: Payoff matrix for two player, three strategy Nash demand game

Three pure strategy Nash equilibria of this game— (High, Low), (Low, Low), and (Medium, Medium). Naturally, egalitarian outcome is (Medium, Medium) irrespective of group. In case of discrimination, one side demands high when interacting with different group's player, and other is forced to go for low. For each strategy i, the proportions in population are given by $x = x_1, x_2, x_3$, and replicator dynamics is given by (similarly for y)

$$\dot{x_i} = x_i(u_i(y) - \sum_{j=0}^{n} u_j(y)x_j)$$

If $p \geq 0.5$ represents population share of majority group, and $(1-p)$ the minority group, then as $(1-p)$ gets smaller, if likelihood of coming at at a lower payoff equilibrium increases, cultural Red King emerges. Regardless of what the opponent is doing, positive payoff is ensured by accommodating. So the groups start to learn to accommodate. But since minority groups learn this lesson more quickly, at some point the majority group begins to learn that they can do better by taking advantage of this accommodating behavior. The dynamics tends to bargaining that advantages the majority.

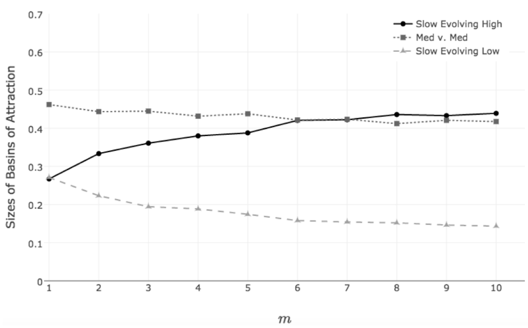


Figure 11: Basins of attraction for 2 populations where one evolves at rate m times the other [O'Connor [2017]]

This analysis explains the need for external stimulus in resource allocation for the minorities, which will be driven to margins as explained by evolutionary game theory.

2.3 Lessons and Limitations

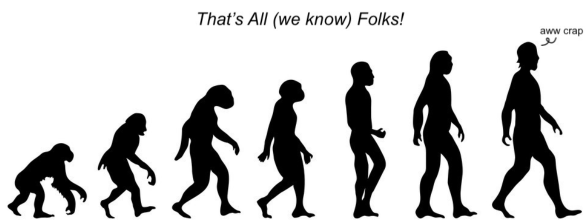
- Rightly called the Renaissance, evolutionary game theory is the branch of economics that has been able to realise the neoclassical dream of scaling up microeconomic one-shot two player games to population dynamics. Additionally, it opens avenues for biologists, engineers and mathematicians for interdisciplinary research because of far reaching implications of the studies.

- While there is a rubrik for solving any problem- constructing a game, finding the ESS, and then replicator dynamics- the lack of structured laws which govern any situation means that every problem has to be addressed separately and that affects the generalisability of the subject is what we feel.

- From what we have studied, evolutionary game theory relies on simulation so far to evaluate population dynamics. While this is a powerful tool to analyse complex and a wide range of scenarios, its disadvantage lies in the fact that it is a numerical technique, and not an exact mathematical solution to the problem. This is the gap which needs to be covered to bring theory closer to practice.

- Specific to Red Queen and Red King effect, the power of these ideas lies in their simplicity to explain complex mechanisms. We felt that the models addressed the elements of a system taken few at a time, which is very useful in identifying causal relationships, but would get tough if the model is not well specified.

- We also felt that social games are better specified, analysed and validated as opposed to biological ones. This might be because of the shorter time span and hence observability of social games. Biological, we felt, was mostly hypothetically explaining certain evolutionary phenomenon, which is logically sound but not validated.



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