

**Review of „Time Delays and Structured Populations in Evolutionary Game Theory” –
Doctoral Thesis by Javad Mohamadichamgavi submitted to the Faculty of
Mathematics, Informatics and Mechanics at the University of Warsaw**

Overview: The formal basis for preparing this review is provided by the provisions of the Act of July 20, 2018, Law on Higher Education and Science, as amended. According to Article 187 of the Act, a doctoral dissertation "presents the candidate's general theoretical knowledge in the discipline as well as the ability to conduct independent scientific work. The subject of the doctoral dissertation is an original solution to a scientific problem or an original solution in terms of the application of the results of one's own scientific research in the economic or social sphere (...), and it may be a written work, including a scientific monograph, a collection of published and thematically related scientific articles, a project, construction, technological, implementation, or artistic work, as well as an independent and distinct part of a collective work."

Summary of my Conclusion: The candidate has presented a written thesis based on a series of six articles published in renowned journals. Five of these were with various co-authors and the remaining paper is a single author paper. These publications present original solutions to problems in the field of evolutionary game theory, which is an interdisciplinary field heavily dependent on mathematical theory and concepts. These publications show that the candidate is very able to apply various fields of mathematics, including game theory, graph theory and dynamical systems. He has worked both individually and in a number of teams. As such, in the opinion of the reviewer, the candidate has clearly met the criteria for being awarded a PhD in the discipline of mathematics. My detailed review of the thesis is given below.

Overview of the Thesis: The thesis is 147 pages long. It is split into two sections. There are three chapters which introduce the mathematical ideas contained in the six published papers which form the basis of the thesis. The introduction contains a bibliography with 99 positions. Each of the papers contain bibliographies with from around 20 to 70 positions. These bibliographies indicate a breadth of knowledge in the fields of game theory, graph theory, evolutionary theory and statistical physics.

Comment: I would have liked to see a short section summarizing the results of the thesis as a whole and suggesting directions for future research. However, the lack of such a section does not detract from the quality of the work presented by the candidate.

Chapter 1 - Introduction: The introduction presents an overview of the development of game theory. It presents the main goals of the thesis, which is to investigate the role of the structure of a population and time delays, such as in the effects of reproduction, within evolutionary processes. The effects of delays can be modelled using delay differential equations or by differentiating between juveniles and adults. The role of population structure is modelled using graph theory. The thesis incorporates six papers that were published in renowned journals in 2024 and 2025. Five of these papers were co-authored with one other author (three with his supervisor, Prof. Miękisz and one each with Prof. Broom and Prof. Bodnar). The sixth paper is a single-author paper by the candidate. The candidate has also published a number of other papers with various co-authors. These papers do not fit into the scope of the doctoral thesis, but indicate that the candidate has a good understanding of the field of evolutionary games and the potential to develop in contingent fields.

Chapter 2 – Introduction to Evolutionary Game Theory: Section 2.1 gives an overview of classical game theory, including the concept of a Nash equilibrium. The candidate presents three types of game that are key to the papers presented in the thesis: i) the Prisoner's Dilemma, ii) the Snowdrift game, iii) the Stag Hunt game. There is some ambiguity in the notation used in the Snowdrift game, since the c used in the line placed after the payoff matrix does not correspond to the c in this payoff matrix, but to the c in Equation (1). It might also have been useful to give a fuller description of the concept of domination for the Prisoner's Dilemma.

Section 2.2 outlines the classical theory of replicator dynamics. It would have been good to give a definition of the concept of an Evolutionarily Stable Strategy (ESS) in this section.

Section 2.3 outlines the theory of replicator dynamics with time delays. Such models can be split into two classes: i) social delay, where individuals react to the profile (set) of strategies used τ time units ago (hence the reproduction rate of individuals using a particular strategy is dependent on the strategy's success τ time units ago and the current frequency of such individuals), ii) biological delay, where new members of the population come from reproduction that occurred τ time units ago (hence the reproduction rate of individuals using a particular strategy is dependent on both the strategy's success and its frequency τ time units ago). Biological delay reflects the fact that offspring need time to mature.

Section 2.4 outlines the Moran process. This is a discrete time process such that at each moment an individual is chosen to reproduce (with a probability proportional a fitness measure) and replaces an individual chosen at random. In structured populations, this individual is chosen at random from the set of neighbours of the reproducing individual.

Section 2.5 presents the core concepts of evolutionary games on graphs with a description of the most commonly used models of reproduction. Section 2.6 describes mean-field approximations and pair approximations, which are later used in combination to approximate the probability of a mutant invading a population.

In the formula for $g(\pi_A, \pi_B)$ on p. 18, l. 3, the coefficient β is missing.

Section 2.7 gives an outline of the relationship between the structure of a population and the evolution of cooperation via compact groups of cooperating individuals.

Chapter 3: Main Results of the Papers – These are outlined below together with a brief outline of the methods used.

Paper 1: Javad Mohamadichamgavi and Marek Bodnar. Bifurcation analysis of replicator dynamics with logistic growth and strategy-dependent time delays in Snowdrift game. *Dynamic Games and Applications*: 1–29 (2025).

Main results: This paper takes into account two factors that have not been considered together in evolutionary games, namely ecological constraints (modelled by the logistic growth of a population) and time delays in replication. The model is based on the Snowdrift game. In such games there is an equilibrium where both Cooperation and Defection coexist. When the delay is strategy independent, this mixed equilibrium is stable as long as the delay is below a value which is proportional to the ratio between the benefit from cooperation and the total cost for cooperation. This leads to a stable population size. For larger delays, the frequencies of the strategies and the size of the population oscillate. If the defectors are delayed, then above a given delay the mixed equilibrium becomes unstable. When co-operators are delayed, then the

2

D M Ramsey

mixed equilibrium is always stable. In the general case, strategy-dependent delays, a wide pattern of bifurcations may be observed.

Methods: This paper considers the social form of delays. The replicator equations are given by two coupled differential equations. One describes the growth of the population as a whole, the other describes the rate of change of the relative frequency of co-operators (and hence, also of defectors). When there are no delays in the replicator dynamics, the relative frequencies of the strategies at the biologically meaningful equilibrium conform to the mixed equilibrium in the Snowdrift game. The corresponding size of the population depends on the average payoff obtained at this equilibrium. The stability of equilibrium points is investigated via linearisation around that point, while the transcendental equation is used to study bifurcations in the system. The analytic results are supported by a range of numerical experiments.

Typing errors: p. 46 before Equation (9) “on the interval $[\tau_M, 0]$ ” should be “on the interval $[-\tau_M, 0]$ ”.

p. 49 Corollary 3: The equilibrium population size is $1/3$, not $1/2$ as stated. This is visible in the phase diagrams.

The paper contains a number of minor misprints, which do not distract from the academic value of the paper (e.g. “exits” instead of “exist” at the bottom of p. 51).

Paper 2: Jacek Miękiś and Javad Mohamadichamgavi. Intrinsic noise in structured replicator dynamics modelling time delays. *Dynamic Games and Applications* 15: 1364–1377 (2025).

Main results: This paper again uses the Snowdrift game. Delays are modelled using a form of life history model. Adults reproduce according to their average reward in the Snowdrift game and offspring mature at a given rate (possibly strategy dependent). A deterministic model of this form can be modelled by a system of four differential equations that give the relative sizes of four subpopulations: two subpopulations of adults each using one of the two strategies in the Snowdrift game and two corresponding subpopulations of juveniles. The authors also consider a stochastic model by assuming that the probabilities of transitions correspond to the appropriate relative rates of transition. When the rate of maturation is not strategy dependent, then the equilibrium frequencies correspond to the mixed Nash equilibrium in the Snowdrift game, although increased delays lead to lower population sizes due to infant mortality. Stochasticity, maybe surprisingly, leads to an increase in the frequency of cooperation, although the equilibrium size of the population decreases. When the rate of maturation is strategy dependent, unsurprisingly, selection favours the strategy associated with the fastest rate of maturation (mortality is strategy independent).

Methods: When there are no delays (individuals are “born as adults”), then the equilibrium point in the deterministic model can be calculated analytically. Numerical results are given for all other cases. The stochastic case (finite population) is modelled using the simulation of a Markov jump process starting with 60 adults (30 using each of the two possible strategies).

Comment: The authors write on p.73 that “the players share the same background fitness...”. It seems to me that “a strategy independent background mortality (possibly differing for adults and juveniles)...” would be a more natural interpretation.

3

D M Ramsey

Question: On p. 79 the formulas for the reproduction rates indicate that the “opponent” in the Snowdrift game is chosen from the entire population, i.e. an individual can play the game with themselves. It is normally assumed in finite population models that the opponent is a different player (another paper included in the thesis uses this “classical” approach). Compared to the classical model, the model used here will favour co-operators. Would increasing a strategy independent delay still lead to an increase in the frequency of cooperation according to the “classical” model?

Paper 3: Javad Mohamadichamgavi and Jacek Miękisz. Effect of the degree of an initial mutant in Moran processes in structured populations. *Physical Review E* 109(4): 044406 (2024).

Main Results: This paper considers how the structure of a population affects the probability of a mutant invading a population and the fixation time. The probability of fixation is decreasing in the degree of a mutant. For a given degree, this probability is greater for Erdős–Rényi (ER) graphs than Barabási–Albert (BA) graphs. However, since low degree nodes are more abundant in BA graphs, the unconditional probability of fixation is greater for BA graphs. The mean time to fixation is higher for BA graphs, while time to fixation (given that fixation occurs) is independent of the degree of the initial mutant.

Methods: The paper uses a Moran model, together with graphs representing the structure of a population of size 500. These graphs are constructed according to the Erdős–Rényi (ER) and Barabási–Albert (BA) procedures. In an ER graph any pair of individuals are connected with probability p . In a BA graph a set of n_0 individuals are connected to each other and then edges to successive individuals are made such that a new individual is connected to a current member of the population with a probability proportional to his/her degree. The parameters p and n_0 are chosen so that the average degree is independent of the type of graph. The relative fitness of a mutant is assumed to be r . Fixation probabilities are estimated using a mean field approximation to estimate transition probabilities once the number of mutants has increased to at least three. The accuracy of these approximations is positively assessed using simulations.

Comment: On p.86 the authors write “At every time step of the process, an individual is chosen with a probability proportional to its fitness and then gives birth to an offspring who inherits its phenotype and replaces a randomly chosen individual”. Should the final “individual” be “neighbour”?

Comment: In the second half of p. 86 the authors describe an approach to approximating the probability of a single mutant expanding to a population of three mutants. The nature of some of these approximations is only described later. For example, on p. 90 it is stated that when going from two mutants to one mutant, the surviving mutant may not be the initial mutant. It would have been better if this description had been given together with Equation (8).

Comment: On p.89 the authors write “In other words, if the process starts from a hub, then, regardless of r , it will soon become extinct”. The authors should add „Given that the process goes extinct”.

Comment: On p. 90 the authors write “For a single mutant to be fixed, the Moran process must pass through the state with j mutants”. This is used to the expected time it takes for a mutant to spread to a population of j given that fixation occurs” in Equation (24). The first equation here is correct. However, the second equation seems to use an analogous (false) argument for the

time to spread to j mutants given that mutants go extinct. I think that the authors wanted to write “given that there are j mutants, for the process to go extinct, then there must be only one mutant at some point in time”. $T_j^e = t_j^e - t_1^e$ would be the appropriate expected time for such a transition.

Typing errors: On p.89 the authors write “if the number of mutants reaches zero, then the extinction probability from this state is zero”. The extinction time is zero, the extinction probability is one.

Question: Of all the papers presented in the thesis, I find the biological interpretation of this model most problematic. If my interpretation is correct, then individuals who are well-connected have by definition a higher mortality rate than those who are only connected to one other individual. This is likely to be unrealistic in many biological scenarios. I think that the results would be completely different if the model was changed so that at each stage the individual to die is chosen at random and then a neighbour is chosen to occupy that position with probabilities proportional to their “fitness”. Please comment on this.

Paper 4: Javad Mohamadichamgavi and Mark Broom. The impact of time delays on mutant fixation in pairwise social dilemma games. *Proceedings of the Royal Society A* 480(2300): 20240195 (2024).

Main Results: This paper looks at the effect of delays in a range of social dilemma games (the Stage-Hunt, Snowdrift and Prisoner’s Dilemma games). Delays make invasion by mutants in the Stage-Hunt game (a co-ordination game) less likely, while invasion becomes more likely in the Snowdrift game (an anti-coordination game). Delays tend to have a negative effect on the probability of co-operators invading in the Prisoner’s Dilemma game.

Methods: The Moran process is used to model the evolution of a finite sized population. The current state is given by the number of mutants in the current moment and τ previous moments, where τ is the delay.

Comment: $\delta_{i,j}$ is not defined in Equation 2.4. It seems to be the Dirac function $\delta_{i,j} = 1$ if and only if $i = j$.

Comment: In the Equation for the absorption time, a_i , one should be added to the right hand side. There is no natural interpretation for the value of $t_{0,N}$ (since fixation cannot occur when the mutant dies out, this value has no effect on the calculation).

Comment: The notation in Equations (4.3) and (4.4) is very strange. It looks like the upper limit of the sums is a set. The sums should be over absorbing and transient states, respectively.

Comment: In Equation (5.1) the ratio r should be inverted. The formula given in the text a couple of lines below is very unclear (there should be brackets around the expression in the denominator). There is a similar formula at the end of this page (p. 107).

Paper 5: Jacek Miękiś and Javad Mohamadichamgavi. Phase transitions in the prisoner’s dilemma game on the Barabási–Albert graph with participation cost. *Physical Review E* 112(3): L032302 (2025).

5

D M Ramsey

Main results: This paper investigates the effect of maintaining links in a BA graph in a network version of the Prisoner's Dilemma game (this version is not classical, since cooperation is only weakly dominated). When these costs are low, cooperation evolves based around hubs. For intermediate costs, cooperation and defection coexist with the population often switching between high and low levels of cooperation. For higher costs of maintaining links, very low levels of cooperation are observed. The critical value of this cost is taken to be the mean of the end points of the intermediate region. This critical value decreases as the relative gain from defection increases. The width of the intermediate region falls as the population size increases, while the midpoint is independent of the population size. However, switching between high and low cooperation regimes remains possible even when the population size become very large.

Method: The model adapts the Prisoner's Dilemma game by introducing costs for maintaining social links. Players in a BA graph play the Prisoner's Dilemma with each of their neighbours and update their strategy based on Fermi's rule (adjusting with a probably based on the difference in payoffs, the constant is chosen so that the strategy with the highest payoff is almost certain to be chosen). There is also a small mutation rate. The evolution of the frequency of cooperation is investigated by simulations and using differential equations that take into account the frequencies of the four possible types of pair. The simulations confirm the relative accuracy of this numerical approach.

Comment: On p. 122, $\lim_{N \rightarrow \infty} \gamma_l(T, N) = \lim_{N \rightarrow \infty} \gamma_l(T, N)$ should be $\lim_{N \rightarrow \infty} \gamma_l(T, N) = \lim_{N \rightarrow \infty} \gamma_r(T, N)$.

Paper 6: Javad Mohamadichamgavi. Strategy-dependent time delays shape cooperation in the spatial prisoner's dilemma game. *Chaos, Solitons & Fractals* 201: 117255 (2025).

Main Results: This article investigates the effect of delays in a Prisoner's Dilemma game played on a regular 200×200 square lattice. Again, defection weakly dominates cooperation. Even when there is a strong incentive to defect, if co-operators are subject to smaller delays than defectors, then the two strategies can coexist. When co-operators are subject to delays, then this delay stabilizes clusters of co-operators when the temptation to defect is small, but not when the temptation to defect is large. On the other hand, when defectors are subject to delays, then exploitation is curbed. Hence, in both regimes co-operation in groups is viable. When defection strongly dominates cooperation, the patterns of evolution are similar, but defection becomes more prevalent.

Method: The results are based on simulation.

Comment: On p. 30 the author writes "cooperation can emerge if cooperators experience shorter delays than defectors. Conversely, if $\tau_C < \tau_D$, the system typically settles into coexistence". I think that " $\tau_C < \tau_D$ " should be " $\tau_C > \tau_D$ ".

Final Summary: Although I have made a number of comments on the thesis, the vast majority of these comments are related to the editing of the thesis and not to the quality of the work. As stated, I conclude that the candidate has clearly met the criteria for being awarded a PhD in the discipline of mathematics.