An Investigation Into Kin Selection and Reciprocal Cooperation in a Viscous Population

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In memory of my grandmother, Ethel Leach (1909 – 1998)

"Hobbes clearly proves, that every creature
Lives in a state of war by nature."

Jonathan Swift, 'On Poetry'

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Abstract

The research presented in this thesis covers several disciplines, bringing together Artificial Intelligence and Artificial Life to answer a question which has more traditionally been the preserve of theoretical biology and sociobiology. More specifically the work presented here applies agent-based simulation and genetic algorithms to investigate the possible mechanisms underlying the evolution of cooperation in populations of self-interested individuals.

The mechanisms proposed and investigated here are from the political and economic sciences, and from theoretical biology. From the political and economic sciences, game theory and particularly the Prisoner's Dilemma suggests a mechanism in the form of reciprocation during repeated interactions among individuals. From theoretical biology, kin selection theory suggests a mechanism in the form of spread of an altruistic trait under genetic control through the benefit it confers on relatives.

This research aims to further the understanding of the relative importance of each of these mechanisms in explaining observed cooperation within populations of self-interested individuals, the circumstances under which each is favoured, and the way in which they interact.

While models investigating cooperation have been designed to use either reciprocal cooperation or kin selection, the study of both mechanisms within the same model has not been carried out. Kin-selected altruism has been suggested as a potential precursor to the evolution of reciprocal cooperation, so the study of both mechanisms together is of interest. Therefore this research presents the design of a model that explicitly supports the operation both of reciprocal cooperation and kin selection. This is achieved by introducing spatial structure to the model, which in conjunction with limited mobility and local interaction and breeding between individuals, has been previously identified as facilitating reciprocal cooperation and kin selection. The model uses 2 x 2 games, primarily the Prisoner's Dilemma, to represent social interaction. Individuals within the model are provided with memories of interaction histories with each other, and conditional strategies that act based on these histories, thus providing scope for reciprocal cooperation. The interaction strategies of individuals are encoded as genotypes in a genetic algorithm, and fitnesses are determined by game payoffs from interactions with other individuals, thus allowing natural selection, including kin selection, to operate on strategies. The model is studied in an attempt to identify the contribution of each mechanism to observed cooperation. As an aid to this investigation, models allowing only the operation of kin selection or reciprocal cooperation are presented and studied. Results from the models are investigated using a combination of analytical, statistical and visualisation techniques.

The main contributions of this research are:

- the design and investigation of a model explicitly supporting the operation of both reciprocal cooperation and kin selection for altruism. This has not been done previously, and is interesting as kin-selected altruism has been suggested as a precursor to the evolution of reciprocal cooperation.

- the analysis of requirements for models supporting only kin-selected altruism in 2 x 2 games. Earlier invocations of kin selection theory have sometimes been weak.
- the analysis of requirements for models supporting only reciprocal cooperation in 2 x 2 games. Earlier models have sometimes inadvertently provided scope for altruism through kin selection.
- the analysis of the operation of, and interaction and dependencies between, kin selection and reciprocal cooperation in 2 x 2 games, revealing in particular the potential for kin selection to act against the evolution of effective strategies for reciprocal cooperation.
- the analysis of the circumstances under which spatial populations favour reciprocal cooperation, revealing a potential force inhibiting the establishment of reciprocal cooperation in such populations.

Contents

ACKNOWLEDGMENTS ..... **I**

ABSTRACT ..... **II**

LIST OF FIGURES ..... **XI**

LIST OF TABLES ..... **XV**

CHAPTER 1 – INTRODUCTION **1**

1.1 INTRODUCTION 1
1.2 ARTIFICIAL INTELLIGENCE AND ARTIFICIAL LIFE 1
1.2.1 Agent-Based Simulation *4*
1.2.2 Genetic Algorithms *5*
1.3 GAME THEORY 7
1.3.1 The Prisoner's Dilemma *8*
1.3.2 Repeated Interaction and the Shadow of the Future *9*
1.3.3 Chicken *10*
1.3.4 Battle of the Sexes *11*
1.3.5 Apology *11*
1.3.6 Hawk-Dove *12*
1.3.7 Games With More Than Two Players *12*
1.3.8 Evolutionary Game Theory *13*
1.3.9 Evolutionary Stable Strategies *13*
1.4 THEORETICAL BIOLOGY 15
1.4.1 Kin Selection *16*
1.4.2 Population Genetical Approaches to Kin Selection *18*
1.4.3 Forces Opposing Kin Selection *19*
1.4.4 Group Selection *20*
1.4.5 Memic Evolution *22*
1.5 MOTIVATION AND AIMS 22
1.6 CONCLUSION 23

CHAPTER 2 – BACKGROUND **24**

2.1 INTRODUCTION 24
2.2 APPROACHES TO STUDYING AND PROMOTING COOPERATION 24
2.2.1 Finite State Automata Approaches *24*
2.2.2 Genetic Algorithm Approaches *25*
2.2.3 Spatial Approaches *26*

2.2.4 Other Approaches *30*
2.3 AXELROD'S TOURNAMENTS AND OTHER REPEATED INTERACTION MODELS 34
2.3.1 Axelrod's Tournaments *34*
2.3.2 Responses to Axelrod's Tournaments *36*
2.3.3 Other Repeated Interaction Models *37*
2.4 KIN SELECTION MODELS 38
2.4.1 Oliphant's Kin Selection Model *38*
2.4.2 Other Kin Selection Models *39*
2.5 CONCLUSION 40

CHAPTER 3 – DESIGN OF MODELS FOR THE INVESTIGATION OF RECIPROCAL COOPERATION AND KIN SELECTION 42

3.1 INTRODUCTION 42
3.2 MOTIVATION FOR THE AGENT-BASED MODELLING APPROACH 42
3.3 THE DESIGN OF A MODEL THAT SUPPORTS KIN SELECTION AND RECIPROCAL COOPERATION 43
3.3.1 Reciprocal Cooperation and the Prisoner's Dilemma *46*
3.3.2 Kin Selection and the Prisoner's Dilemma *48*
3.4 THE DESIGN OF A MODEL THAT SUPPORTS ONLY KIN SELECTION 50
3.5 THE DESIGN OF A MODEL THAT SUPPORTS ONLY RECIPROCAL COOPERATION 52
3.5.1 Existing Reciprocal Cooperation Models *52*
3.5.2 Reciprocal Cooperation Without Kin Selection in an Evolutionary Model *52*
3.6 A NOTE ON THE GENETIC MODEL USED 52
3.7 CONCLUSION 54

CHAPTER 4 – IMPLEMENTATION OF THE PROPOSED MODELS 55

4.1 INTRODUCTION 55
4.2 ENVIRONMENT IMPLEMENTATION 55
4.2.1 Evolutionary Prisoner's Dilemma and Pure Kin Selection Models *55*
4.2.2 Pure Reciprocal Cooperation Model *56*
4.2.3 A Note on the Topology Used *56*
4.3 AGENT IMPLEMENTATION 57
4.3.1 Memory Description *57*
4.3.2 Genotype Description *57*
4.3.3 Energy Level Description *58*
4.4 MODEL OPERATION 58
4.4.1 Update Ordering in the Model *59*
4.4.2 Asynchronous Updating in the Model *60*
4.5 EXPERIMENTAL CONFIGURATIONS 60
4.5.1 General Model Configuration *61*

4.5.2 Experimental Mode Configuration *61*
4.6 OBSERVATION 61
4.6.1 Measurements of Relatedness *61*
4.6.2 Visualisation of Kin Selection *62*
4.6.3 Experimental Mode Observation *64*
4.6.4 Observer Mode Observation *64*
4.7 CONCLUSION 65

CHAPTER 5 – RESULTS 66

5.1 INTRODUCTION 66
5.2 DEFINITION OF RESULTS COLLECTED 66
5.2.1 Average Cooperation Level *67*
5.2.2 Average Relatedness Level *67*
5.2.3 Average Number of Interactions *68*
5.2.4 Average Run Length *68*
5.2.5 Average Cell Population *68*
5.2.6 Average Lifetime Opponents *68*
5.3 RESULTS FROM THE EVOLUTIONARY PRISONER'S DILEMMA IN THE ABSENCE OF SELECTION 69
5.3.1 Description *69*
5.3.2. Results *69*
5.4 RESULTS FROM THE EVOLUTIONARY PRISONER'S DILEMMA 71
5.4.1 Description *71*
5.4.2 Results *71*
5.4.3 Results at Low Movement Probabilities *73*
5.4.4 Results at Very Low Movement Probabilities *75*
5.5 RESULTS FROM THE PURE KIN SELECTION MODEL 76
5.5.1 Description *76*
5.5.2 Results *76*
5.5.3 Results at Low Movement Probabilities *77*
5.5.4 Results at Very Low Movement Probabilities *78*
5.5.5 Results with Long Agent Lifespan *79*
5.6 RESULTS FROM THE PURE RECIPROCAL COOPERATION MODEL 80
5.6.1 Description *80*
5.6.2 Results *80*
5.6.3 Results with Long Agent Lifespan *82*
5.7 RESULTS OF LOCAL POPULATION REGULATION 84
5.7.1 Description *84*
5.7.2 Results from the Evolutionary Prisoner's Dilemma with Local Population Regulation *84*
5.7.3 Results from the Pure Kin Selection Model with Local Population Regulation *87*

5.8 Results from the Evolutionary Prisoner's Dilemma with Modifications from Oliphant's Model 88
5.8.1 Defector-Disadvantageous Payoffs *88*
5.8.2 One-Dimensional Environment *90*
5.9 Results from the Extended Interaction Length Evolutionary Prisoner's Dilemma 92
5.9.1 Description *92*
5.9.2 Results *93*
5.10 Results from the Evolutionary Prisoner's Dilemma Using Battle of the Sexes Payoffs 94
5.10.1 Description *94*
5.10.2 Results *94*
5.11 Model Visualisation 96
5.11.1 Visualisation of the Evolutionary Prisoner's Dilemma *96*
5.11.2 Visualisation of the Pure Kin Selection Model *98*
5.11.3 Visualisation of the Pure Reciprocal Cooperation Model *100*
5.12 Conclusion 103

CHAPTER 6 – DISCUSSION 104

6.1 Introduction 104
6.2 The Importance of Kin Selection in the Models Studied 104
6.2.1 Hamilton's Rule *104*
6.2.2 Inclusive Fitness *105*
6.2.3 A Force Opposing Kin Selection for Altruism in the Prisoner's Dilemma *107*
6.3 The Importance of Reciprocal Cooperation in the Models Studied 108
6.3.1 The Collective Stability of Tit-for-Tat *108*
6.3.2 A Mathematical Model of Expected Interaction Length *110*
6.3.3 Conditions Which Favour Reciprocal Cooperation *113*
6.3.4 A Variant on the Evolutionary Prisoner's Dilemma *115*
6.4 Discussion of the Contributions of Kin Selection and Repeated Interaction to Observed Cooperation 116
6.4.1 Definition of Correlation Calculations *116*
6.4.2 Investigation of Results from the Evolutionary Prisoner's Dilemma *117*
6.4.3 Investigation of Results from the Evolutionary Prisoner's Dilemma with Local Population Regulation *119*
6.4.4 Comparison of Results from the Evolutionary Prisoner's Dilemma with Results from the Pure Kin Selection Model *122*
6.4.5 Investigation of Results from the Pure Kin Selection Model *122*
6.4.6 Investigation of Results from the Pure Kin Selection Model with Local Population Regulation *124*

6.4.7 Comparison of Results from the Evolutionary Prisoner's Dilemma with Results from the Pure Reciprocal Cooperation Model ... *125*
6.4.8 Investigation of Results from the Pure Reciprocal Cooperation Model ... *126*
6.4.9 Discussion of Visualisations ... *128*
6.4.10 Discussion of Results from the Evolutionary Prisoner's Dilemma, Pure Kin Selection and Pure Reciprocal Cooperation Models ... *129*
6.4.11 A Note on the Difficulty of Separating Kin Selection and Reciprocal Cooperation in the Prisoner's Dilemma ... *131*
6.4.12 The Interaction of Kin Selection and Reciprocal Cooperation in the Prisoner's Dilemma . *131*
6.5 DISCUSSION OF OTHER RESULTS ... 132
6.5.1 Effects of Local Population Regulation ... *132*
6.5.2 Cognitive Requirements for the Iterated Prisoner's Dilemma ... *133*
6.5.3 Results from the Battle of the Sexes ... *134*
6.5.4 Results from the One-Dimensional Evolutionary Prisoner's Dilemma ... *135*
6.6 A NOTE ON THE BEHAVIOUR OF THE MODELS WITH NO MOBILITY ... 135
6.7 CONCLUSION ... 136

CHAPTER 7 – CONCLUSIONS AND FURTHER WORK ... 138

7.1 INTRODUCTION ... 138
7.2 SUMMARY OF THE RESEARCH ... 138
7.3 REVIEW OF THE RESEARCH METHODOLOGY ... 139
7.4 SUMMARY OF CONTRIBUTIONS ... 140
7.5 FURTHER WORK ... 141
7.5.1 Modification of the Models ... *141*
7.5.2 Investigation of Unusual Results ... *142*
7.5.3 Exploration of Parameters ... *142*
7.5.4 Fitness Visualisation ... *143*
7.5.5 Alternative Interaction Models ... *143*
7.6 CONCLUSION ... 144

REFERENCES ... 146

GLOSSARY OF BIOLOGICAL TERMS ... 156

GLOSSARY OF GAME THEORETICAL TERMS ... 158

GLOSSARY OF SYMBOLS ... 159

APPENDIX A – INVESTIGATING THE MECHANISMS UNDERLYING COOPERATION IN VISCOUS POPULATION MULTI-AGENT SYSTEMS ... 162

APPENDIX B – OBJECTIVE C SOURCE FOR THE EVOLUTIONARY PRISONER'S DILEMMA 168

MAKEFILE 168
EPDDEFINES.H 168
MAIN.M 169
EPDEXPERIMENTSWARM.H 169
EPDEXPERIMENTSWARM.M 170
EPDOBSERVERSWARM.H 174
EPDOBSERVERSWARM.M 175
EPDSWARM.H 177
EPDSWARM.M 178
EPDAGENT.H 182
EPDAGENT.M 182
EPDWORLD.H 190
EPDWORLD.M 191
DOUBLEDATA.H 203
DOUBLEDATA.M 203
INTEGERDATA.H 203
INTEGERDATA.M 203
EXPERIMENT.SETUP 204
PAYOFFS.SETUP 204
WORLD.SETUP 204

APPENDIX C – SAMPLE USER INTERFACE FOR THE OBSERVER MODE OF THE EVOLUTIONARY PRISONER'S DILEMMA 205

APPENDIX D – EXPERIMENTAL DATA 206

EXPERIMENT 5.3.2 206
EXPERIMENT 5.4.2 210
EXPERIMENT 5.4.3 213
EXPERIMENT 5.4.4 217
EXPERIMENT 5.5.2 221
EXPERIMENT 5.5.3 225
EXPERIMENT 5.5.4 229
EXPERIMENT 5.5.5 233
EXPERIMENT 5.6.2 237
EXPERIMENT 5.6.3 240
EXPERIMENT 5.7.2 244
EXPERIMENT 5.7.3 248

EXPERIMENT 5.8.1 252
EXPERIMENT 5.8.2 256
EXPERIMENT 5.9.2 260
EXPERIMENT 5.10.2 264

List of Figures

FIGURE 1.1. EXECUTION OF A TYPICAL GENETIC ALGORITHM 5
FIGURE 1.2. THE OPERATION OF THE PARAMETERISED CROSSOVER OPERATOR 6
FIGURE 1.3. THE OPERATION OF THE INVERSION OPERATOR 6
FIGURE 2.1. A FINITE STATE AUTOMATON FOR THE STRATEGY TIT-FOR-TAT 24
FIGURE 2.2. REPRODUCTION OF NOWAK & MAY'S (1993) PRISONER'S DILEMMA CELLULAR AUTOMATA. 28
FIGURE 3.1. ALTRUISTIC BENEFIT TO A RELATIVE IN THE SINGLE-ITERATION PRISONER'S DILEMMA WITH ROLES 51
FIGURE 4.1. THE EXECUTION SEQUENCE OF THE EVOLUTIONARY PRISONER'S DILEMMA 58
FIGURE 4.2. COLOUR CHART FOR CELL POPULATIONS IN VISUALISATION 63
FIGURE 4.3. A SAMPLE VISUALISATION OF COOPERATION AND RELATEDNESS IN A SPATIAL POPULATION 64
FIGURE 5.1. AVERAGE COOPERATION IN THE EPD WITHOUT SELECTION 69
FIGURE 5.2. AVERAGE RELATEDNESS IN THE EPD WITHOUT SELECTION 70
FIGURE 5.3. AVERAGE NUMBER OF INTERACTIONS IN THE EPD WITHOUT SELECTION 70
FIGURE 5.4. AVERAGE LIFETIME OPPONENTS IN THE EPD WITHOUT SELECTION 71
FIGURE 5.5. AVERAGE COOPERATION IN THE EPD 71
FIGURE 5.6. AVERAGE RELATEDNESS IN THE EPD 72
FIGURE 5.7. AVERAGE RELATEDNESS ON LOCI SUBJECT TO KIN SELECTION IN THE EPD 72
FIGURE 5.8. AVERAGE NUMBER OF INTERACTIONS IN THE EPD 73
FIGURE 5.9. AVERAGE LIFETIME OPPONENTS IN THE EPD 73
FIGURE 5.10. AVERAGE COOPERATION IN THE EPD AT LOW MOVEMENT PROBABILITIES 74
FIGURE 5.11. AVERAGE RELATEDNESS AT LOCI SUBJECT TO KIN SELECTION IN THE EPD AT LOW MOVEMENT PROBABILITIES 74
FIGURE 5.12. AVERAGE NUMBER OF INTERACTIONS IN THE EPD AT LOW MOVEMENT PROBABILITIES ... 75
FIGURE 5.13. AVERAGE COOPERATION IN THE EPD AT VERY LOW MOVEMENT PROBABILITIES 75
FIGURE 5.14. AVERAGE RELATEDNESS ON LOCI SUBJECT TO KIN SELECTION IN THE EPD AT VERY LOW MOVEMENT PROBABILITIES 76
FIGURE 5.15. AVERAGE NUMBER OF INTERACTIONS IN THE EPD AT VERY LOW MOVEMENT PROBABILITIES 76
FIGURE 5.16. AVERAGE COOPERATION IN THE PURE KIN SELECTION MODEL 77
FIGURE 5.17. AVERAGE RELATEDNESS IN THE PURE KIN SELECTION MODEL 77
FIGURE 5.18. AVERAGE COOPERATION IN THE PURE KIN SELECTION MODEL AT LOW MOVEMENT PROBABILITIES 78
FIGURE 5.19. AVERAGE RELATEDNESS IN THE PURE KIN SELECTION MODEL AT LOW MOVEMENT PROBABILITIES 78

FIGURE 5.20. AVERAGE COOPERATION IN THE PURE KIN SELECTION MODEL AT VERY LOW MOVEMENT PROBABILITIES 79
FIGURE 5.21. AVERAGE RELATEDNESS IN THE PURE KIN SELECTION MODEL AT VERY LOW MOVEMENT PROBABILITIES 79
FIGURE 5.22. AVERAGE COOPERATION IN THE PURE KIN SELECTION MODEL WITH LONG AGENT LIFESPAN 80
FIGURE 5.23. AVERAGE RELATEDNESS IN THE PURE KIN SELECTION MODEL WITH LONG AGENT LIFESPAN 80
FIGURE 5.24. AVERAGE COOPERATION IN THE PURE RECIPROCAL COOPERATION MODEL 81
FIGURE 5.25. AVERAGE RELATEDNESS IN THE PURE RECIPROCAL COOPERATION MODEL 81
FIGURE 5.26. AVERAGE NUMBER OF INTERACTIONS IN THE PURE RECIPROCAL COOPERATION MODEL 81
FIGURE 5.27. AVERAGE LIFETIME OPPONENTS IN THE PURE RECIPROCAL COOPERATION MODEL 82
FIGURE 5.28. AVERAGE COOPERATION IN THE PURE RECIPROCAL COOPERATION MODEL WITH LONG AGENT LIFESPAN 82
FIGURE 5.29. AVERAGE RELATEDNESS IN THE PURE RECIPROCAL COOPERATION MODEL WITH LONG AGENT LIFESPAN 83
FIGURE 5.30. AVERAGE NUMBER OF INTERACTIONS IN THE PURE RECIPROCAL COOPERATION MODEL WITH LONG AGENT LIFESPAN 83
FIGURE 5.31. AVERAGE LIFETIME OPPONENTS IN THE PURE RECIPROCAL COOPERATION MODEL WITH LONG AGENT LIFESPAN 84
FIGURE 5.32. AVERAGE COOPERATION IN THE EPD WITH LOCAL POPULATION REGULATION 85
FIGURE 5.33. AVERAGE RELATEDNESS ON LOCI SUBJECT TO KIN SELECTION IN THE EPD WITH LOCAL POPULATION REGULATION 85
FIGURE 5.34. AVERAGE NUMBER OF INTERACTIONS IN THE EPD WITH LOCAL POPULATION REGULATION 86
FIGURE 5.35. AVERAGE RUN LENGTH IN THE EPD WITH LOCAL POPULATION REGULATION 86
FIGURE 5.36. AVERAGE LIFETIME OPPONENTS IN THE EPD WITH LOCAL POPULATION REGULATION 86
FIGURE 5.37. AVERAGE COOPERATION IN THE PURE KIN SELECTION MODEL WITH LOCAL POPULATION REGULATION 87
FIGURE 5.38. AVERAGE RELATEDNESS IN THE PURE KIN SELECTION MODEL WITH LOCAL POPULATION REGULATION 87
FIGURE 5.39. AVERAGE RUN LENGTH IN THE PURE KIN SELECTION MODEL WITH LOCAL POPULATION REGULATION 88
FIGURE 5.40. AVERAGE COOPERATION IN THE EPD WITH OLIPHANT'S PAYOFFS 89
FIGURE 5.41. AVERAGE RELATEDNESS IN THE EPD WITH OLIPHANT'S PAYOFFS 89
FIGURE 5.42. AVERAGE NUMBER OF INTERACTIONS IN THE EPD WITH OLIPHANT'S PAYOFFS 90
FIGURE 5.43. AVERAGE LIFETIME OPPONENTS IN THE EPD WITH OLIPHANT'S PAYOFFS 90
FIGURE 5.44. AVERAGE COOPERATION IN THE ONE-DIMENSIONAL EPD 91

FIGURE 5.45. AVERAGE RELATEDNESS IN THE ONE-DIMENSIONAL EPD 91
FIGURE 5.46. AVERAGE NUMBER OF INTERACTIONS IN THE ONE-DIMENSIONAL EPD 92
FIGURE 5.47. AVERAGE LIFETIME OPPONENTS IN THE ONE-DIMENSIONAL EPD 92
FIGURE 5.48. AVERAGE COOPERATION IN THE EPD WITH EXTENDED INTERACTION LENGTH 93
FIGURE 5.49. AVERAGE NUMBER OF INTERACTIONS IN THE EPD WITH EXTENDED INTERACTION LENGTH 93
FIGURE 5.50. AVERAGE COOPERATION IN THE EPD WITH BATTLE OF THE SEXES PAYOFFS 95
FIGURE 5.51. AVERAGE RELATEDNESS IN THE EPD WITH BATTLE OF THE SEXES PAYOFFS 95
FIGURE 5.52. AVERAGE NUMBER OF INTERACTIONS IN THE EPD WITH BATTLE OF THE SEXES PAYOFFS . 96
FIGURE 5.53. VISUALISATION OF THE EPD AT MOVEMENT PROBABILITY 1 97
FIGURE 5.54. VISUALISATION OF THE EPD AT MOVEMENT PROBABILITY 0.5 97
FIGURE 5.55. VISUALISATION OF THE EPD AT MOVEMENT PROBABILITY 0.1 98
FIGURE 5.56. VISUALISATION OF THE EPD AT MOVEMENT PROBABILITY 0.01 98
FIGURE 5.57. VISUALISATION OF THE PURE KIN SELECTION MODEL AT MOVEMENT PROBABILITY 1 99
FIGURE 5.58. VISUALISATION OF THE PURE KIN SELECTION MODEL AT MOVEMENT PROBABILITY 0.5 99
FIGURE 5.59. VISUALISATION OF THE PURE KIN SELECTION MODEL AT MOVEMENT PROBABILITY 0.1 .. 100
FIGURE 5.60. VISUALISATION OF THE PURE KIN SELECTION MODEL AT MOVEMENT PROBABILITY 0.01 100
FIGURE 5.61. VISUALISATION OF THE PURE RECIPROCAL COOPERATION MODEL AT MOVEMENT PROBABILITY 1 101
FIGURE 5.62. VISUALISATION OF THE PURE RECIPROCAL COOPERATION MODEL AT MOVEMENT PROBABILITY 0.5 101
FIGURE 5.63. VISUALISATION OF THE PURE RECIPROCAL COOPERATION MODEL AT MOVEMENT PROBABILITY 0.1 102
FIGURE 5.64. VISUALISATION OF THE PURE RECIPROCAL COOPERATION MODEL AT MOVEMENT PROBABILITY 0.01 102
FIGURE 6.1. RELATIVE INCLUSIVE FITNESS OF COOPERATION AND DEFECTION ALLELES 106
FIGURE 6.2. RELATEDNESS THRESHOLD FOR ALTRUISM FAVOURED BY KIN SELECTION 107
FIGURE 6.3. EXPECTED NUMBER OF INTERACTIONS IN THE EPD 111
FIGURE 6.4. EXPECTED NUMBER OF INTERACTIONS IN THE PURE RECIPROCAL COOPERATION MODEL WITH LONG AGENT LIFESPAN 112
FIGURE 6.5. EXPECTED NUMBER OF INTERACTIONS IN THE PURE RECIPROCAL COOPERATION MODEL .. 112
FIGURE 6.6. MAXIMUM LOCAL POPULATION SIZE REQUIRED FOR COLLECTIVE STABILITY OF TIT-FOR-TAT IN THE EPD 114
FIGURE 6.7. SCATTER PLOT OF AVERAGE COOPERATION AGAINST AVERAGE NUMBER OF INTERACTIONS IN THE EPD AT MOVEMENT PROBABILITIES 0 TO 1 WITH INTERVAL 0.1 118
FIGURE 6.8. SCATTER PLOT OF AVERAGE COOPERATION AGAINST AVERAGE NUMBER OF INTERACTIONS IN THE EPD AT MOVEMENT PROBABILITY 0.1 119

FIGURE 6.9. SCATTER PLOT OF AVERAGE COOPERATION AGAINST AVERAGE RELATEDNESS IN THE EPD WITH LOCAL POPULATION REGULATION AT MOVEMENT PROBABILITIES 0 TO 1 WITH INTERVAL 0.1 120
FIGURE 6.10. SCATTER PLOT OF AVERAGE COOPERATION AGAINST AVERAGE NUMBER OF INTERACTIONS IN THE EPD WITH LOCAL POPULATION REGULATION AT MOVEMENT PROBABILITIES 0 TO 1 WITH INTERVAL 0.1 120
FIGURE 6.11. SCATTER PLOT OF AVERAGE RELATEDNESS AGAINST AVERAGE NUMBER OF INTERACTIONS IN THE EPD WITH LOCAL POPULATION REGULATION AT MOVEMENT PROBABILITIES 0 TO 1 WITH INTERVAL 0.1 121
FIGURE 6.12. SCATTER PLOT OF AVERAGE COOPERATION IN THE EPD AGAINST AVERAGE COOPERATION IN THE PURE KIN SELECTION MODEL AT MOVEMENT PROBABILITIES 0 TO 1 WITH INTERVAL 0.1 .. 122
FIGURE 6.13. SCATTER PLOT OF AVERAGE COOPERATION AGAINST AVERAGE RELATEDNESS IN THE PURE KIN SELECTION MODEL AT MOVEMENT PROBABILITIES 0 TO 1 WITH INTERVAL 0.1 123
FIGURE 6.14. SCATTER PLOT OF AVERAGE COOPERATION AGAINST AVERAGE RELATEDNESS IN THE PURE KIN SELECTION MODEL AT MOVEMENT PROBABILITY 0.7 124
FIGURE 6.15. SCATTER PLOT OF AVERAGE COOPERATION IN THE EPD AGAINST AVERAGE COOPERATION IN THE PURE RECIPROCAL COOPERATION MODEL AT MOVEMENT PROBABILITIES 0 TO 1 WITH INTERVAL 0.1 126
FIGURE 6.16. SCATTER PLOT OF AVERAGE COOPERATION AGAINST AVERAGE NUMBER OF INTERACTIONS IN THE PURE RECIPROCAL COOPERATION MODEL AT MOVEMENT PROBABILITIES 0 TO 1 WITH INTERVAL 0.1 127
FIGURE 6.17. SCATTER PLOT OF AVERAGE COOPERATION AGAINST AVERAGE NUMBER OF INTERACTIONS IN THE PURE RECIPROCAL COOPERATION MODEL AT MOVEMENT PROBABILITY 0.1 128

List of Tables

TABLE 1.1. PRISONER'S DILEMMA PAYOFF MATRIX 9
TABLE 1.2. CHICKEN PAYOFF MATRIX 10
TABLE 1.3. BATTLE OF THE SEXES PAYOFF MATRIX 11
TABLE 1.4. APOLOGY PAYOFF MATRIX 11
TABLE 1.5. HAWK-DOVE PAYOFF MATRIX 12
TABLE 3.1. ONE-DIMENSIONAL STRATEGY SPECIFICATION 47
TABLE 3.2. TWO-DIMENSIONAL STRATEGY SPECIFICATION 47
TABLE 1.1 REPRODUCTION. PRISONER'S DILEMMA PAYOFF MATRIX 48
TABLE 3.3. SINGLE-ITERATION PRISONER'S DILEMMA PAYOFFS BETWEEN RELATIVES 48
TABLE 3.4. SINGLE-ITERATION PRISONER'S DILEMMA PAYOFFS BETWEEN NON-RELATIVES 49
TABLE 3.2 REPRODUCTION. TWO-DIMENSIONAL STRATEGY SPECIFICATION 57
TABLE 4.1. COLOUR DESCRIPTIONS OF CELL POPULATIONS IN VISUALISATION 63
TABLE 5.1. MODEL CONFIGURATION FOR THE EPD WITHOUT SELECTION 69
TABLE 5.2. OLIPHANT'S PRISONER'S DILEMMA PAYOFF MATRIX 88
TABLE 5.3. BATTLE OF THE SEXES PAYOFF MATRIX 94
TABLE 6.1. A TWO-DIMENSIONAL STRATEGY TO ALTERNATE DEFECTION WITH COOPERATION 109
TABLE 6.2. CORRELATION OF RESULTS IN THE EVOLUTIONARY PRISONER'S DILEMMA 117
TABLE 6.3. CORRELATION OF AVERAGE COOPERATION WITH AVERAGE NUMBER OF INTERACTIONS AT DIFFERENT MOVEMENT PROBABILITIES IN THE EPD 118
TABLE 6.4. CORRELATION OF RESULTS IN THE EVOLUTIONARY PRISONER'S DILEMMA WITH LOCAL POPULATION REGULATION 120
TABLE 6.5. CORRELATION OF AVERAGE COOPERATION WITH AVERAGE NUMBER OF INTERACTIONS AT DIFFERENT MOVEMENT PROBABILITIES IN THE EPD WITH LOCAL POPULATION REGULATION 121
TABLE 6.6. CORRELATION OF AVERAGE COOPERATION WITH AVERAGE RELATEDNESS AT DIFFERENT MOVEMENT PROBABILITIES IN THE PURE KIN SELECTION MODEL 123
TABLE 6.7. CORRELATION OF AVERAGE COOPERATION WITH AVERAGE RELATEDNESS AT DIFFERENT MOVEMENT PROBABILITIES IN THE PURE KIN SELECTION MODEL WITH LOCAL POPULATION REGULATION 125
TABLE 6.8. CORRELATION OF AVERAGE COOPERATION WITH AVERAGE NUMBER OF INTERACTIONS AT DIFFERENT MOVEMENT PROBABILITIES IN THE PURE RECIPROCAL COOPERATION MODEL 127
TABLE 6.9. CORRELATION OF RESULTS IN THE EVOLUTIONARY PRISONER'S DILEMMA WITH BATTLE OF THE SEXES PAYOFFS 134

Chapter 1 – Introduction

1.1 Introduction

The research presented in this thesis covers several disciplines, bringing together Artificial Intelligence and Artificial Life to answer a question which has more traditionally been the preserve of theoretical biology and sociobiology. More specifically the work presented here applies agent-based simulation and genetic algorithms to investigate the possible mechanisms underlying the evolution of cooperation in populations of self-interested individuals. The mechanisms proposed and investigated here are from the political and economic sciences, and from theoretical biology. From the political and economic sciences, game theory and particularly the Prisoner's Dilemma, as popularised by Axelrod (1984), suggests a mechanism in the form of reciprocation during repeated interactions among individuals. From theoretical biology, kin selection theory, as summarised in Hamilton's (1964a, 1964b) inclusive fitness rule, suggests a mechanism in the form of spread of an altruistic trait under genetic control through the benefit it confers on relatives. This research aims to further the understanding of the relative importance of each of these mechanisms in explaining observed cooperation within populations of self-interested individuals, the manner in which they interact, and the circumstances under which each is favoured.

1.2 Artificial Intelligence and Artificial Life

In the same way that Artificial Intelligence seeks to study and even create intelligence in machines, so Artificial Life seeks to study and even create life itself in artificial media, such as computers.

> "*The term Artificial Life literally means 'life made by humans rather than by nature.*'" (Langton, 1995).

The above statement was made by Christoper G. Langton, one of the pioneers of Artificial Life (AL), in the introduction to his book "Artificial Life: An Overview", which presented contributions from Artificial Life experts in an attempt to define the field. Probably the earliest example of Artificial Life was presented by von Neumann (1966) who constructed self-replicating systems with the computational power of Universal Turing Machines in a cellular automaton. Langton (1984) developed this research, and by removing the requirement for computational equivalence with Universal Turing Machines, greatly simplified the self-replicating systems involved by reducing both the number of cells they occupied, and the number of distinct cell states required by them.

As part of the attempt to define Artificial Life, Taylor & Jefferson (1995) considered the potential for applying Artificial Life to open problems in biology. Taylor & Jefferson classified Artificial Life applications according to the medium used; whether "wetware", experimenting with actual biological substances such as molecules of ribonucleic acid; software, using computer simulation; or hardware, using physical robots situated in a real environment. Taylor & Jefferson also discussed the use of Artificial Life to model populations compared to the more traditional use of equational models. Taylor &

Jefferson considered that the Artificial Life approach to modelling populations was to represent them procedurally, as concurrently executing computer programs, stating that they "*[...] consider […] the representation of organisms by programs, to be the defining feature of 'artificial life' models of population behaviour, the property that distinguishes them from other mathematical or computational models of populations*". Taylor & Jefferson argued that equational population models were subject to some serious limitations in their frequent assumptions of very large populations, the size of the equations necessary to represent even a simple organism's behaviour, and their difficulty in dealing with the highly nonlinear effects that frequently occur in animal behaviour. Furthermore they argued that, by encoding an organism's behaviour explicitly in an Artificial Life model, it was easier to modify the model to take account of new hypotheses than was the case with equational models. Taylor & Jefferson concluded their consideration of Artificial Life as a tool for biological inquiry by presenting some of the open questions in biology that they considered to be suitable for study using Artificial Life techniques, including the origin of life and self-organisation, cultural evolution, the origin and maintenance of sex, and the evolution of the mind in nature.

Ray (1995) considered a different facet of Artificial Life, that of Artificial Life as the instantiation of life processes. Ray argued that it was possible to create "*disembodied but genuine instances of specific properties of life in artificial systems*" and that separating out some property of life that was of interest made it easier to manipulate that property and observe its behaviour. In instantiating life processes in an artificial medium Ray advocated the following fundamental principle:

> "*to understand and respect the natural form of the [medium], to facilitate the process of generating forms that are adapted to the [...] medium, and to let evolution find forms and processes that naturally exploit the possibilities inherent in the medium.*"

Ray's approach to instantiating life processes in a digital computer was demonstrated in Tierra. Tierra is a variant on machine code designed to be more robust than normal machine code, so that errors in machine code programs are handled gracefully, rather than causing the system executing that code to crash. Tierra is also designed to reduce the mapping from the huge number of possible bit patterns used in specifying a machine instruction onto the set of legal machine instructions. These modifications to standard machine code are necessary to reduce its sensitivity to the random modification that typically occurs in evolution, and therefore render it evolvable. The Tierra system then is one in which evolution occurs by the execution of special machine code programs, which replicate themselves as part of their execution, and compete with each other for the finite resources of processor time and memory. Ray considered how phenomena present in organic life could be expressed in this digital medium, such as sexual reproduction, genetic parasites, the evolution of cellularity and the evolution of multicellularity.

Bonabeau & Theraulaz (1995) offered yet another definition of Artificial Life as part of their consideration of its benefits and pitfalls:

> "*[...] a general method consisting in generating at a macroscopic level, from microscopic, generally simple, interacting components, behaviours that are* ***interpretable as lifelike***." (emphasis authors')

Among the problems Bonabeau & Theraulaz identified were the danger of equating phenomena observed in different classes of system, such as fractal patterns of bacteria growth and electrochemical deposition, and the importance of recognising arbitrary boundary conditions from outside the system under investigation as being potentially important to evolution within the system. They also considered the benefits of Artificial Life for biology, engineering and art. Of particular interest to the research presented here, Bonabeau & Theraulaz discussed the position of Artificial Life in relation to theoretical biology, introduced later in this chapter. They argued that Artificial Life is not in competition with theoretical biology, but that it complements theoretical biology by going beyond pure biological modelling.

As the disparate views presented above indicate, the definition of Artificial Life is not consolidated. More recently Artificial Life has been defined as:

> "*an interdisciplinary research enterprise investigating the fundamental properties of living systems by means of the simulation and synthesis of life-like processes in artificial media*" (Bedau, 2000).

In fact the question of whether Artificial Life typically involves synthesis or simulation of living systems is the subject of ongoing debate. Noble et al (2000) summarised one such debate that raised the questions of what scientists from other disciplines want from Artificial Life, and whether Artificial Life provides new ways of thinking about problems or whether it simply should provide additional empirical data to extend investigations into natural phenomena. Subsequently Di Paolo et al (2000) reviewed previous attempts to describe the scientific role of Artificial Life simulations, which were broadly divided into the "emergent thought experiment" approach of Bedau (1999) and the "physics model" approach of Kitano, Hamahashi et al (1997). The "emergent thought experiment" approach treats computer simulations as a method of extending traditional thought experiments into areas in which the human mind cannot apprehend the implications of the premises of the original thought experiment, such as complex systems. Whereas in a traditional thought experiment, the conclusions follow intuitively from the premises, in an "emergent thought experiment" the conclusions "emerge" non-intuitively from the premises. However Di Paolo et al criticised the "emergent thought experiment" approach due to Bedau's assertion that such experiments "*can explain how some phenomenon occurs only if [they produce] actual examples of the phenomena in question, it is not sufficient to produce something that represents the phenomenon but lacks its essential properties.*" They argued that Bedau's experiments could not be thought experiments, as only empirical experiments are sources of empirical data, however if they did not act as sources of empirical data then they could not meet Bedau's requirement for producing "*examples of the phenomena in question*". The "physics model" approach of Kitano, Hamahashi et al (1997) uses results from computer simulations to generate new hypotheses, which are then validated experimentally. However the "physics model" approach first requires that any computer simulation be validated against empirical results to confirm that it correctly implements the theory under investigation. Di Paolo et al argued that this validation process cannot be carried out satisfactorily as any disagreement between the results from the computer simulation and empirical results could either mean that the simulation does not implement the theory correctly, or could equally mean that the theory has been implemented correctly but is in itself

incorrect. Di Paolo et al therefore proposed that computer simulations be regarded as opaque thought experiments, in which it is necessary to conduct theoretical investigations into the simulation model in order to understand how it generates phenomena, rather than simply labelling these phenomena as "emergent". The understanding generated by this theoretical investigation can then be used to further understand existing theoretical frameworks.

The approach taken in this thesis will be to consider the model under investigation as an "opaque thought experiment", as defined by Di Paolo et al (2000).

1.2.1 Agent-Based Simulation

> "*ā'gent n. 1. one who or that which exerts power or produces an effect*" (Concise Oxford Dictionary)

Wooldridge & Jennings (1994) provide two definitions of agency, a weak definition and a strong definition. In the weak definition, an agent is a hardware or software based computer system with the properties of autonomy, social ability, reactivity and pro-activeness. Autonomy means that the agent operates without the direct intervention of humans or others. Social ability means that the agent interacts with other agents. Reactivity means that the agent perceives their environment, and responds to changes that occur in that environment. Pro-activeness means that the agent, in addition to simple response, is able to exhibit goal-directed behaviour by taking the initiative. An example of weak agency could be a team of robot football players (Kitano, Asada et al, 1997). Each member of the team would exhibit social ability through their ability to pass the ball between each other, call for the ball, and so forth. Each team member would be reactive as they would perceive their position, their teammates' positions, and the position of the ball, and act on this information. Team members would also be able to exhibit goal-directed behaviour, for example passing the ball to a teammate in a better position, with the goal of scoring a point for the team.

In the strong definition an agent is "*a computer system that, in addition to having the properties [ascribed to weak agency], is either conceptualised or implemented using concepts that are more usually applied to humans.*" Such concepts include knowledge, belief, intention, obligation, and even emotion. An example of strong agency is provided in Wright and Sloman's (1997) MINDER1 model, in which protoemotional agents are implemented.

The weak definition described above is closest to what is intended in this thesis by the term "agent", although even the weak definition is more stringent than the definition intended here, for which pro-activeness is not a requirement.

Wooldridge & Jennings also make the distinction between "intelligent agents" that maintain symbolic models of the world and use complex symbolic reasoning, and agents with "reactive architectures", which do not. While the motivation for studying "intelligent agents" is clear in the context of classical Artificial Intelligence, the benefit of studying agents with "reactive architectures" is less obvious. In fact, the interest and usefulness of studying such simple agents as those with "reactive architectures" comes in one instance when they are studied in the context of an agent-based simulation. In an agent-based simulation, a group of agents inhabit a common environment, and interact with each other within this

environment. From the repeated simple interactions of agents, complex dynamics can emerge. The study of these dynamics is the motivation for using an agent-based simulation, as identified by Bonabeau & Theraulaz (1995) in the previous section.

1.2.2 Genetic Algorithms

Genetic algorithms were initially designed for solving optimisation problems (Box, 1957; Bremermann, 1962, among others). Holland (1975) broadened their use to the study of adaptive systems, these being systems in which populations of individuals or species co-evolve with each other. Genetic algorithms apply the techniques of natural evolution in searching through a parameter space, whether that parameter space is a representation of a static optimisation problem, or a representation of a dynamic co-evolution problem. The characteristics of natural evolution that genetic algorithms implement are differential survival of individuals in a population, according to their fitness under some criteria, and heritable variation of traits having an effect on those individuals' fitness.

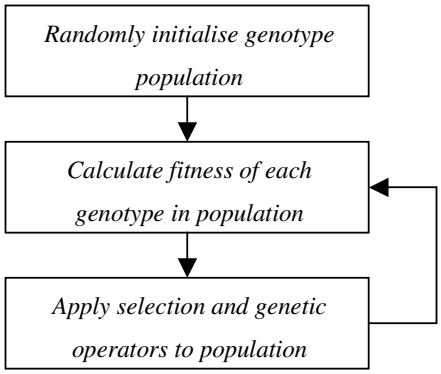

Figure 1.1. Execution of a Typical Genetic Algorithm

Figure 1.1 above presents the execution of a typical genetic algorithm. A genetic algorithm is composed of a population of individuals. Each individual's characteristics are encoded onto its genotype. The population is usually initialised before running the genetic algorithm, by randomly assigning values at each point on each individual's genotype. The points on the genotype are known collectively as loci, while the different valid values for each locus are known as alleles. The first step in the genetic algorithm is to assess the fitness of each individual in the population against some fitness criteria. Each individual's fitness results in part from its characteristics as encoded on its genotype.

The next step in the genetic algorithm is to select the fittest individuals in the population to reproduce. Selection may be as simple as selecting the fittest half of the population, or may be more complex, for example selecting each individual with a certain probability weighted according to their fitness. Reproduction can be either sexual or asexual. Asexual reproduction involves cloning the parent individual's genotype to produce an offspring genotype. During asexual cloning, a mutation operator is applied which introduces a small probability of changing the value at each point on the offspring's genotype so that it differs from the value on it's parent's genotype at the corresponding point.

Sexual reproduction involves two individuals recombining sections of their genotypes, using a crossover operator, to generate an offspring genotype. As in asexual reproduction, the mutation operator can be

applied to the offspring's genotype to change the values of some of the points on its genotype. An inversion operator can also be used during reproduction, in which a section of the offspring's genotype is reversed. The purpose of this operator is to allow points on the genotype which function well together to be moved closer to each other, reducing the risk of separation by the crossover operator. In order for the inversion operator to preserve the meaning of the information encoded on genotypes, its implementation requires interpretation of each point on the genotype to be independent of that point's position on the genotype. This is in contrast to genetic algorithms that do not use the inversion operator, which can simply interpret each point on the genotype according to its position. The inversion operator is not frequently used in genetic algorithms, perhaps due to the expense of implementing a more complex genotype interpretation mechanism.

Having reproduced, the individuals in the population are typically discarded and their offspring form the next generation, whose members are again assessed for fitness and reproduced. The process continues ad infinitum, or until a satisfactory solution is found to the problem the genetic algorithm is being used to solve.

Representations of two of the genetic operators are presented in figures 1.2 and 1.3 below. Figure 1.2 shows parameterised crossover (Spears and DeJong, 1991), while figure 1.3 illustrates inversion. The genotypes in figures 1.2 and 1.3 encode strategies for the iterated Prisoner's Dilemma, which is introduced in section 1.3. Each point on the genotypes specifies a "cooperate" (C) or "defect" (D) action for different previous outcomes of playing the Prisoner's Dilemma against an opponent. In figure 1.3 the numbers are the labels necessary for correct interpretation of genotypes that are subjected to the inversion operator.

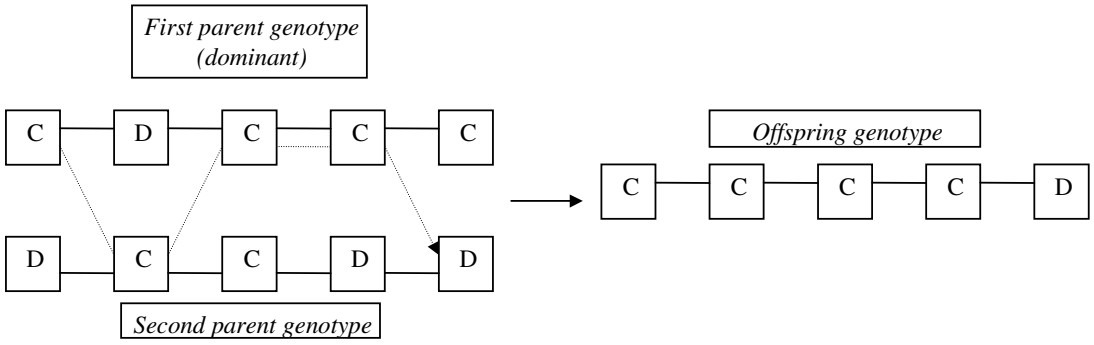

Figure 1.2. The Operation of the Parameterised Crossover Operator

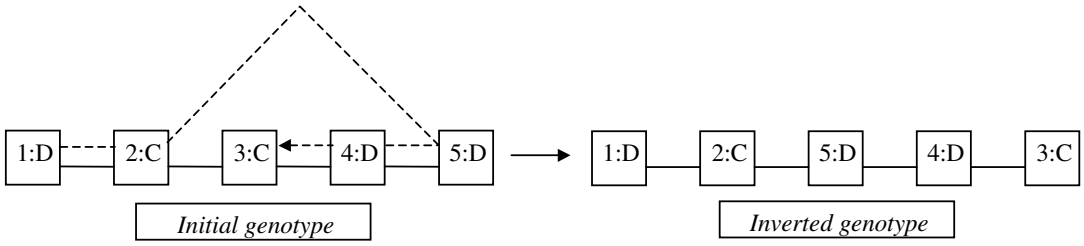

Figure 1.3. The Operation of the Inversion Operator

Genetic algorithms have been applied to model many adaptive systems, such as the human immune system (Smith et al, 1993). Mitchell (1996) continued such work, applying genetic algorithms to the field of Artificial Life. Corno et al (1998a, 1998b) have applied kin selection theory, described in section 1.4.1, to genetic algorithms used in algorithmic optimisation. Mitchell & Forrest (1994) provide a good summary of applications of genetic algorithms in the field of Artificial Life.

Genetic algorithms have been widely used in models of social interaction, such as those typically investigated using the Prisoner's Dilemma and other 2 x 2 games described in the next section, with varying degrees of success. Chattoe (1998), however, has criticised some applications of evolutionary algorithms, including genetic algorithms, in the field of social science. Some of the concerns Chattoe raised arise from the origins of genetic algorithms in the field of optimisation. Chattoe argued for relative fitness between individuals in a population, rather than an externally imposed fitness function that provides a system-wide goal. This concern has already been addressed in many models in which fitness results from interactions between agents, such as Holland's (1975) Echo model. Chattoe also criticised the lack of distinction between genotype and phenotype in many evolutionary models. Chattoe's arguments were based on the need to use evolutionary algorithms in a way that is conceptually the same as biological evolution in order to study meaningfully the evolution of social processes. As well as agreeing with Chattoe's concern over relative fitness and the distinction between genotype and phenotype, Mitchell & Forrest (1994) identified problems with making quantitative relationships between genetic algorithm simulations and the systems they purport to model, as well as the effect of the choice of genetic representations and operators on the behaviour of genetic algorithms. Mitchell & Forrest also argued that the most obvious area for genetic algorithm research to be extended to is the study and understanding of evolutionary systems.

1.3 Game Theory

"*cō-ŏperā'tion n. working together to same end*" (Concise Oxford Dictionary)

The study of cooperation is motivated by the question of why self-interested entities such as humans should cooperate when doing so may not appear to be in their interests. Game theory provides theoretical tools for investigating the behaviour of self-interested individuals, and this section introduces the field and its concepts. Definitions of these concepts are also presented in a glossary at the end of this thesis.

Axelrod (1984) popularised the study of cooperation with his book "The Evolution of Cooperation" and in doing so established the Prisoner's Dilemma as the predominant model of social cooperation in the following years of research. As will be described in section 1.3.1, the Prisoner's Dilemma captures the situation in which two individuals always improve their individual welfare by acting selfishly, yet if both individuals follow this reasoning, they share in an outcome that is worse than if they had both acted cooperatively.

The Prisoner's Dilemma belongs to a class of games in game theory that are known as "2 x 2 games". They are so called because they involve two participants, who each have a choice of two actions. Rapoport & Guyer (1966) described 2 x 2 games as the simplest conceivable form of game, as it takes at

least two players, each with a choice of action, to make a game. Rapoport & Guyer presented a taxonomy of the 78 distinct 2 x 2 games, and presented game theoretical considerations of their solutions.

Continuing this work, Rapoport (1967) identified the four most interesting 2 x 2 games, these being symmetric non-trivial games. A symmetric game is one in which the payoffs from the game are the same from the point of view of each player. A non-trivial game is a game in which players choosing the action that gives the best payoff regardless of the other's action do not achieve the largest available payoff. The games Rapoport identified as being of interest can be labelled The Prisoner's Dilemma, Chicken, Battle of the Sexes and Apology, and these games are presented in the following sections. In addition to these games, the Hawk-Dove game is also presented, which originates from the development of the field of evolutionary game theory, described in section 1.3.8. All of these games can also be labelled as non zero-sum games, where such a game is one in which a gain by one player does not necessarily mean a corresponding loss by the other. Such games can be contrasted with zero-sum games such as chess, where a gain by one player necessarily implies a loss for the other.

Guyer & Rapoport (1972) have presented an experimental study of the distinct 2 x 2 games when played once by human subjects. Their results showed that naïve players responded to changes in the payoff matrices of strategically equivalent games, and also that "maximin" strategies were predominant among such players. A "maximin" strategy is one designed to minimise the player's loss if such a loss should occur.

1.3.1 The Prisoner's Dilemma

The Prisoner's Dilemma was conceived by Flood & Dresher at the RAND Corporation in about 1950, and formalised shortly afterwards by A. W. Tucker. However it was Axelrod (1984) who really raised interest in the Prisoner's Dilemma as a model of social interaction suitable for studying cooperative behaviour. The Prisoner's Dilemma receives its name from the following scenario: two prisoners in custody, accomplices in a crime, have two options each: to inform on the other (defect), or to refuse to incriminate their accomplice (cooperate). The prisoners are imprisoned separately and have no way of communicating with each other, so each has to choose how to act without knowing the action their accomplice has chosen. If one prisoner informs on the other, while the other keeps quiet, the informer is let off "scot-free" by the authorities, while the other receives the maximum sentence. If both inform on each other, both receive a medium sentence, but if both keep quiet, both are sentenced to the minimum time in prison. Their dilemma is this; each receives a lighter sentence, and so improves their situation, by informing on the other. However, if both follow this logic and inform on each other they each receive the medium sentence, when by remaining mutually silent they could both have received the lightest sentence.

The dilemma faced by the prisoner's in the scenario above arises because informing is a Nash equilibrium (Nash, 1950, 1951). A Nash equilibrium is a strategy that is a best reply to itself, meaning that no other strategy will give a higher payoff against the Nash equilibrium strategy than it receives against itself. In the example above, the payoffs are the lengths of the sentences received by each player, with a shorter sentence corresponding to a higher payoff, while the strategies are informing or not

informing. However, the Nash equilibrium for the Prisoner's Dilemma is also a deficient equilibrium, meaning that there exists some other outcome of the game in which both players get larger payoffs (Rapoport & Guyer, 1966) A typical Prisoner's Dilemma payoff matrix that captures this equilibrium is presented in table 1.1 below. The payoff matrix specifies players' payoffs, or rewards, for different outcomes in the game, according to both players' actions. The different payoffs are classified as follows: the payoff for defecting (D) when an opponent cooperates (C) is known as the "temptation" (***T***), the payoff for cooperating when an opponent defects is known as the "sucker's payoff" (***S***), the payoff for mutual cooperation is known as the "reward" (***R***), and finally the payoff for mutual defection is known as the "penalty" (***P***).

	C	**D**
C	3,3	0,5
D	5,0	1,1

Table 1.1. Prisoner's Dilemma Payoff Matrix

(note: payoffs to the row player are listed first)

As can be seen from the payoff matrix in table 1.1 above, mutual defection is a Nash equilibrium because the only alternative strategy to defection, namely cooperation, receives a lower payoff when played against defection than defection does when played against itself. However it can also be seen from table 1.1 that mutual defection is the sub-optimal outcome for both players.

The values in a Prisoner's Dilemma matrix can be varied as desired, but in order to preserve the characteristics of the Prisoner's Dilemma, the following conditions must be satisfied: the temptation must be greater than the reward, which must be greater than the penalty, which in turn must be greater than the sucker's payoff. Additionally the reward must be greater than half the sum of the temptation and the sucker's payoff. More formally, the following must hold:

$$T > R > P > S$$

$$R > (T + S)/2$$

It should be noted that the second requirement for the Prisoner's Dilemma was not identified in Guyer's (1967) definition, due to the use of an ordinal payoff scale.

1.3.2 Repeated Interaction and the Shadow of the Future

Although the Nash Equilibrium of the Prisoner's Dilemma is mutual defection, Trivers (1971) proposed repeated interaction as a mechanism to support cooperation, and subsequently Axelrod (1984) introduced the concept of the "shadow of the future", based on Shubik's (1970) work. The shadow of the future is defined as the probability that two individuals will interact again at some point in the future. If the shadow of the future is large then iterated interaction is likely, and so cooperation is favoured. If, however, the shadow of the future is small, then single iteration encounters are common, and so defection is favoured. Axelrod described the shadow of the future in terms of the discount parameter ***w***, which is "*the degree to which the payoff of each move is discounted relative to the previous move*", so that the discounted payoff from an interaction at ***t*** interactions in the future is obtained by multiplying the

payoff by w^t. For example, a payoff T at 5 interactions in the future gives a discounted payoff of T (w^5), so if T = 5 and w = 0.95, the discounted payoff is 5 (0.95^5) = 3.87. Similarly, the cumulative payoff for a sequence of rewards R is $R + wR + w^2R \ldots = R / (1 - w)$ (Axelrod, 1984).

Axelrod proposed that spatial organisation of a population could increase the shadow of the future sufficiently for cooperation to dominate. In a spatial population with local interaction, individuals interact with their neighbours, a relatively unchanging subset of the entire population. As the candidates for interaction are reduced from the situation where individuals can interact with any other individual in the entire population, interactions between the same individuals become more frequent, thus increasing the shadow of the future.

1.3.3 Chicken

The payoff matrix for the "Game of Chicken" (Rapoport & Chammah, 1966) is presented in table 1.2 below. This game can be conceptualised as a game of chicken played by two people, each driving a car. The aim is to swerve at the last possible moment, and so avoid the other car. There are three possible scenarios; both players swerve (choose A), one player swerves (chooses A) while their opponent drives straight (chooses B), or both players drive straight (choose B). In the first instance, both players receive a modest payoff. In the second instance, the swerving player receives a penalty (a loss of prestige in this example) while their opponent receives a large payoff (a gain in prestige). In the third instance, both players receive a penalty from the obviously undesirable situation of driving into each other!

	A	**B**
A	1,1	-1,2
B	2,-1	-2,-2

Table 1.2. Chicken Payoff Matrix

(note: payoffs to the row player are listed first)

Chicken belongs to a class of games labelled as "pre-emption games" by Rapoport & Guyer (1966). In contrast to the Prisoner's Dilemma there is no Nash Equilibrium for Chicken. Instead there is an incentive for each player to be the first to pre-empt by choosing B while the other player chooses A, resulting in an equilibrium outcome. An equilibrium outcome is one in which neither player can change their choice, while the other player's choice remains constant, without decreasing their payoff. In fact the equilibria in Chicken can be described as Pareto-equilibria meaning that there is no other outcome in the game, other than the equilibria, for which both players get larger payoffs (Rapoport & Guyer, 1967). A Pareto-equilibrium is the opposite of a deficient equilibrium, such as that identified in the Prisoner's Dilemma game above. As the first player to pre-empt in Chicken gains a larger payoff at the expense of the other player, the pre-empting player can be labelled the "exploiter" (Rapoport, 1967). Obviously, despite the pressure to be the first to pre-empt in Chicken, the situation of both players pre-empting simultaneously is mutually undesirable, as described in the anecdote above.

1.3.4 Battle of the Sexes

The payoff matrix for the "Battle of the Sexes" (Rapoport, 1966) is presented below in table 1.3. This game can be described by the situation where a man and woman both have different preferences for an evening's entertainment. For each player, their preferred choice is A, however both players also receive some reward for participating in the same activity as their partner, even if it is not their own preferred activity. The worst case involves both players choosing their partner's favourite entertainment (B), so both players spend an evening without their partner, doing something they don't enjoy. Alternatively both players can choose their own favourite entertainment (A). This results in both players doing something they enjoy, but not receiving the reward from their partner's company. For the last alternative, one of the players must choose their partner's preferred entertainment (B), while that partner also chooses their own preferred entertainment (A). In this case the player choosing their partner's favourite entertainment receives a higher payoff, which could reflect their partner's gratitude to them, and is sometimes known as the "leader" (Rapoport, 1967).

	A	**B**
A	-1,-1	1,2
B	2,1	-2,-2

Table 1.3. Battle of the Sexes Payoff Matrix

(note: payoffs to the row player are listed first)

Battle of the Sexes, like Chicken, is a pre-emption game. However in Battle of the Sexes the first player to pre-empt increases the payoffs of both players, while giving the larger payoff to themself. For this reason, Battle of the Sexes can also be called "Benevolent Chicken" (Rapoport & Guyer, 1966). As in Chicken, the danger of both players pre-empting simultaneously remains.

1.3.5 Apology

The payoff matrix for "Apology" is presented below in table 1.4. This game can be thought of as a situation where two people have quarrelled. Both will benefit if one apologises to the other (by choosing A), but the apologiser will pay some penalty in the form of "loss of face". However if both chose to apologise at once, neither will be rewarded. One can imagine that both people simultaneously go to the other's house, only to find they are not at home. Yet this situation is still better than if both refuse to apologise (by choosing B).

	A	**B**
A	-1,-1	2,1
B	1,2	-2,-2

Table 1.4. Apology Payoff Matrix

(note: payoffs to the row player are listed first)

Apology is identical to the Battle of the Sexes except that the player who pre-empts first gives the largest payoff to the other player, rather than themself. For this reason the pre-empting player can be called the "martyr" (Rapoport, 1967).

1.3.6 Hawk-Dove

The "Hawk-Dove" game (Maynard Smith, 1982) is intended to capture the situation where two animals are contesting a resource with a certain value. Each animal has three available behaviours, "display", "escalate", and "retreat". Retreating abandons the resource to the opponent, displaying does not injure the opponent while escalating may do. Two strategies for this game are available, hawk (H) and dove (D). A hawk will escalate and continue to do so until it is either injured or its opponent retreats. A dove will display, but retreat as soon as its opponent escalates. In the case where two hawks interact, both will escalate until one is injured and the other takes the resource. If a hawk and a dove interact, the dove will retreat without injury, leaving the resource to the hawk. If two doves interact, they will either share the resource, or perhaps waste time displaying if it is indivisible. These possibilities are reflected in the payoff matrix shown in table 1.5 below. In this matrix, ***V*** represents the fitness value of the resource, and ***C*** represents the fitness cost of an injury sustained.

	H	**D**
H	$\frac{1}{2}(V-C)$	*V*
D	0	*V/2*

Table 1.5. Hawk-Dove Payoff Matrix

(note: payoffs to the row player are shown)

It is interesting to note that if the cost ***C*** is less than the value ***V*** then the Hawk-Dove game with averaged payoffs is equivalent to a Prisoner's Dilemma without the condition ***R*** > (***T*** + ***S***) / 2. This can be seen by observing that, as long as ***V*** – ***C*** is positive and non-zero, then

$$V > \frac{V}{2} > \frac{1}{2}(V-C) > 0$$

Equating the payoffs ***V*** with ***T***, ***V*** / 2 with ***R***, (***V*** – ***C***) / 2 with ***P*** and 0 with ***S*** gives the condition for the Prisoner's Dilemma ***T*** > ***R*** > ***P*** > ***S***. Then it can be seen that, providing ***C*** is less than ***V***, the Hawk-Dove payoff matrix presented above in table 1.5 is also the payoff matrix for the Prisoner's Dilemma, with the hawk and dove strategies corresponding to the Prisoner's Dilemma strategies of defect and cooperate respectively. As noted above, the requirement ***R*** > (***T*** + ***S***) / 2 for the Prisoner's Dilemma is not satisfied by this payoff matrix, however a slight modification, changing the payoff 0 to –1, satisfies this requirement while preserving the spirit of the original Hawk-Dove game.

1.3.7 Games With More Than Two Players

Although not considered here, games with more than two participants are possible and can prove interesting to study. Akiyama & Kaneko (1995) investigated an iterated three-player non zero-sum game of coalition formation. In this game groups of three players were able to receive payoffs by forming coalitions of two players, while excluding the third player, however an attempt to form a coalition by three players resulted in no payoffs for any of the players. Akiyama & Kaneko studied the evolution of variable length deterministic strategies for this game and discovered evolution began with differentiation

of players by class, in which some strategies were able to successfully exploit others. Temporal differentiation of players followed, in which players evolved strategies to cycle their membership of coalitions, thus distributing the payoffs from coalition membership more equitably. Evolution proceeded by diversifying and increasing the complexity of the strategies in the population, resulting in a population of coexisting strategies with different complexities and periods of coalition membership. Akiyama & Kaneko concluded that the evolutionary dynamics and resulting complexity and variation in their model had not been found in models using two player games such as the iterated Prisoner's Dilemma.

1.3.8 Evolutionary Game Theory

Traditionally when considering a 2 x 2 game, game theory makes the assumption of fully rational individuals playing the game in order to decide on the equilibrium outcome of the game. Assuming that players in a game are rational means that it is assumed that each player both knows the structure of the game, and assumes that the other player is also rational and knows the structure of the game. In this case, the equilibrium outcome of the game is that which results when each player makes the rational choice. An example of the solution of a 2 x 2 game assuming rational players is the Nash Equilibrium of the Prisoner's Dilemma. As noted in section 1.3.1, regardless of the action of the opponent, an individual playing the Prisoner's Dilemma always improves their payoff by defecting instead of cooperating. A rational player, knowing this fact, and assuming that their opponent is also rational and also knows this fact, therefore defects. Thus if two rational players engage in the Prisoner's Dilemma, the outcome is mutual defection, which unfortunately is sub-optimal but inescapable.

Many species, however, manage to solve 2 x 2 games without being rational. In fact even the assumption of full rationality in human beings is questionable, as human beings are frequently known to act irrationally. For example Guyer & Rapoport (1972) presented results from a study of human subjects in which the subjects changed their strategy choices between strategically equivalent games, apparently due to differences in the magnitude of the game payoffs. Maynard Smith (1982) introduced the concept of evolutionary game theory, which dispensed with the requirement for rationality among players by allowing the solutions of 2 x 2 games to come about through the action of evolution on populations of players. Weibull (1995) provides a more recent overview of the field. The Hawk-Dove game (Maynard Smith, 1982) presented in section 1.3.6, is one such game that has received an evolutionary game theory treatment, giving rise to the concept of the Evolutionary Stable Strategy described in the next section.

1.3.9 Evolutionary Stable Strategies

The Evolutionary Stable Strategy (Maynard Smith & Price, 1973; Maynard Smith, 1974, 1982) is a central concept in evolutionary game theory. An Evolutionary Stable Strategy is "*a strategy such that, if most of the members of a population adopt it, there is no 'mutant' strategy that would give higher reproductive fitness*" (Maynard Smith & Price, 1973). For example, if a population consists entirely of individuals using the strategy of pure defection in the Prisoner's Dilemma, then no individual playing a different strategy against that population will receive a better payoff than the individuals using the pure defection strategy (Axelrod, 1984). More formally, an Evolutionary Stable Strategy is one that meets the

following conditions, where $\boldsymbol{x}$ and $\boldsymbol{y}$ are strategies and $\boldsymbol{u}(\boldsymbol{x}, \boldsymbol{y})$ is the payoff of strategy $\boldsymbol{x}$ when played against strategy $\boldsymbol{y}$ (Weibull, 1995)

$$u(y,x) \leq u(x,x) \qquad \forall y$$

$$u(y,x) = u(x,x) \Rightarrow u(y,y) < u(x,y) \quad \forall y \neq x$$

Evolutionary Stable Strategies originally arose to explain such phenomena as restraint in animal conflict (Maynard Smith & Price, 1973) without the need for the kind of group selection arguments described in section 1.4.4. In the terminology of dynamical systems an Evolutionary Stable Strategy is asymptotically stable (Weibull, 1995), meaning that if the population starts from a state close to the Evolutionary Stable Strategy it will converge to the Evolutionary Stable Strategy. However, despite this, Evolutionary Stable Strategies do not provide information on how that state is reached from any given initial state of the population.

Evolutionary Stable Strategies can either be pure or mixed. A pure Evolutionary Stable Strategy is one in which a single pure strategy such as Hawk is employed by the entire population. A Mixed Evolutionary Stable Strategy is one in which either a mixture of two or more pure strategies, such as Hawk and Dove, coexist stably in the population at a certain ratio, or individuals in the population each employ a mixture of two or more pure strategies, with a certain ratio of probabilities. In their original study of restraint in animal conflict Maynard Smith & Price (1973) showed that no pure strategy was an Evolutionary Stable Strategy in the Hawk-Dove game. Instead they found that Mixed Evolutionary Stable Strategies existed, which could occur either at the population level or at the individual level.

Several of the approaches described in this thesis will present models that refer to Evolutionary Stable Strategies. Fogel et al (1997) have argued that the assumptions of infinite population and averaged payoffs, used to generate Evolutionary Stable Strategies, weaken them as an explanation for finite population behaviour. In particular this implies that Evolutionary Stable Strategies are not practically attainable in finite populations with random payoffs based on individual encounters. Rather, chaotic behaviour should be expected in such models. However, Ficici & Pollack (2000) have investigated Fogel et al's findings and shown that they result from the choice of selection mechanisms. Ficici & Pollack demonstrated how the selection mechanisms used by Fogel et al gave rise to the results presented and that these results were insufficiently explained by the use of finite populations and non-averaged payoffs. Ficici & Pollack went on to show how the use of Stochastic Universal Sampling (Baker, 1987) as a selection mechanism could lead to Evolutionary Stable Strategies in finite populations. They concluded that the choice of selection mechanism has important consequences for the dynamics of an evolutionary system.

Deakin (1966) presented a mathematical study of a spatial model based on sub-populations, showing that such a model provided sufficient conditions for polymorphism of genotypes. A polymorphism of genotypes is a population state in which several different genotypes co-exist within the population. A genotype is the genetic blueprint used to encode an individual's physical and behavioural characteristics, and could be considered to correspond to the different strategies of Hawk and Dove in Maynard Smith's

(1982) model. Deakin's conclusion can therefore be considered to support the existence of Mixed Evolutionary Stable Strategies,

Boyd & Lorberbaum (1987) proved that no strategy in the Prisoner's Dilemma that is fully determined by its history up to interaction t is evolutionarily stable if:

$$w > \min[(T-R)/(T-P),(P-S)/(R-S)]$$

where `min` evaluates to the lowest of the two values in brackets.

Grafen (1979) investigated Evolutionary Stable Strategies in the Hawk-Dove game when played between relatives, first considered by Maynard Smith (1978). Grafen determined that the mixed strategy case, in which strategies were defined as probabilities of behaving as Hawks or Doves, and the pure strategy case, required separate treatments. Grafen also identified that previous studies into Evolutionary Stable Strategies were incorrect, due to their usage of fitness instead of gene frequency.

1.4 Theoretical Biology

The field of theoretical biology is concerned with understanding the mechanisms of evolution and natural selection. Darwin (1859) first advocated natural selection as the mechanism responsible for the complexity and suitability of animals to live in the environments they inhabit. Darwin outlined the fundamental conditions necessary for evolution by natural selection to operate as being self-replication in a finite environment with heritable variation. Under these conditions the fittest individuals in a population, defined as those most successful at competing for the resources required for reproduction within their finite environment, reproduce offspring that inherit some of the aspects that contributed to the increased fitness of their parents. Probably the most commonly applied tool of theoretical biology is population genetics, an area of theoretical biology concerned with mathematical modelling of the dynamics of gene frequencies in populations undergoing selection. A much-used example of population genetics is Price's (1970, 1972) formulation of natural selection and covariance. A more sophisticated method within population genetics is found in quantitative genetics, which takes account of some of the complexities of real evolution such as environmental effects, and genes whose effects are not independent, for example through dominance or epistasis. For example, Crowe & Nagylaki (1976) presented a model of selection, based on Price's (1970, 1972) equations, that took account of dominance and epistasis without assuming random mating or linkage equilibrium. Population genetics and quantitative genetics provide powerful tools for predicting the behaviour of populations under evolutionary pressure, however they encounter some problems in dealing with some of the complications of real populations, such as finite populations and structured populations.

In this thesis reference will be made to concepts from the fields of biology and theoretical biology. Definitions of some of these concepts are presented in a glossary at the end of this thesis. Additionally Maynard Smith (1998) provides a more detailed overview of population and quantitative genetics.

1.4.1 Kin Selection

In addition to reciprocal cooperation, another possible mechanism to explain cooperative behaviour and even altruism can be found in Hamilton's (1964a, 1964b) theory of kin selection. There is one fundamental condition for the operation of kin selection, that the behaviour of an individual has an effect on the reproductive success of its relatives. Hamilton introduced what has become known as Hamilton's rule, which states that an altruistic gene will be selected for when

$$\frac{c}{b} < r$$

where ***c*** is the cost in fitness of an altruistic act to the actor, ***b*** is the benefit in fitness to the recipient of the altruistic act, and ***r*** is the coefficient of relationship between the actor and recipient. This coefficient of relationship is effectively the probability that the recipient of an altruistic act contains the altruistic gene that is causing the donor to act altruistically.

Traditionally individuals had been considered to maximise their individual fitness, which is their reproductive fitness measured in terms of the number of offspring they produce. Hamilton's rule states that individuals will maximise a quantity known as inclusive fitness, which is "*the animal's production of offspring[…] stripped of all components[…] due to the individual's social environment, leaving the fitness he would express if not exposed to any of the harms or benefits of that environment, […] and augmented by certain fractions of the quantities of the harm and benefit the individual himself causes to the fitnesses of his neighbours. The fractions in question are simply the coefficients of relationship[…]*" (Hamilton, 1964a). Usefully Grafen (1984) identified erroneous definitions of inclusive fitness that have been proposed in the past, such as that of Wilson (1975), which incorrectly include those offspring of the individual and the individual's relatives which that individual has not had an effect on.

The coefficient of relationship between individuals was expected by Maynard Smith (1976) to be dependent on those individuals being relatives, such as siblings or cousins. Maynard Smith considered that other causes for a high coefficient of relationship at an altruistic locus were unlikely, as they would require that the altruistic gene also determine association between individuals. This explanation has also been proposed by Dawkins (1976) in the form of the "green beard effect", in which a hypothetical gene causes the bearer to have a green beard, while also directing altruism to other individuals with green beards. The "green beard effect" had already been mentioned by Hamilton (1964b). A gene with multiple effects, such as the green beard gene, is described as pleitropic. While pleitropic genes do exist, and such genes could undoubtedly direct altruism to copies of themselves in the gene pool, both Maynard Smith and Dawkins considered that the chances of the same gene both specifying some identifying label and also directing altruism to individuals with that label were very small.

Kin selection theory can be applied in spatial environments where there is local movement and interaction of agents, and where agents reproduce using evolutionary algorithms. The local movement and interaction in such models leads to interactions among related agents. Such interactions will favour cooperative behaviour, because cooperation promotes the survival of relatives who probably share the "gene" for such cooperative behaviour. To use Hamilton's (1964a) words "*we would expect to find*

giving traits commonest and most highly developed in the species with the most viscous populations whereas uninhibited competition should characterise species with the most freely mixing populations."

West Eberhard (1975) presented a thorough investigation of kin selection, reformulating Hamilton's rule to take account of altruism by descendents, to be valid from the point of view of any member of a population other than the donor or recipient of altruism, and also to have a classical and an inclusive fitness component. West Eberhard also considered how the cost / benefit ratio was of significance in kin selection calculations, and how sufficiently high cost / benefit ratios could support altruism between less related individuals. Additionally, West Eberhard considered parental manipulation and mutually beneficial altruism as alternative explanations for altruism. In particular, West Eberhard noted that kin selection and reciprocal altruism are likely under the same conditions, such as low dispersal rate and stable group formation, among others.

Grafen (1984) identified several assumptions present in Hamilton's (1964a, 1964b) rule; that costs and benefits are additive, that gene frequency among potential donors and recipients is the same, and that selection is weak. The most fundamental assumption is the additivity of costs and benefits. If this assumption is violated then the theory underlying inclusive fitness is invalidated at a fundamental level. The assumption of identical gene frequency among donors and recipients can be simply restated as the assumption that relatedness means what it is intended to mean, namely the degree of genetic similarity at the locus under consideration. Similarly the assumption of weak selection pertains to relatedness, and is required to ensure that ancestry is a sufficiently accurate indicator of the degree of relatedness. If this assumption is violated then the direction of selection is still given by Hamilton's rule, but the strength of selection predicted by the rule may be incorrect.

Michod & Anderson (1979) considered the appropriate measures of the coefficient of relationship for use with Hamilton's rule. Michod & Anderson noted that the coefficient of relationship is not required for models based on changes in gene frequency, but that it is required in order to apply kin selection theory to real populations. They identified limitations in the use of Wright's (1922) coefficient of relationship and Hamilton's (1971) coefficient of relatedness, and proposed an alternative probabilistic measure of genetic relatedness between two individuals, with components due to common ancestry and due to population gene frequency.

Grafen (1985a) also considered how to measure the coefficient of relationship, noting that members of the same population usually share a high percentage of their genes, approximately 80% in humans according to Cavalli-Sforza & Bodmer (1971), yet this does not mean that the coefficient of relationship used when applying Hamilton's rule to humans should be 0.8. Therefore, according to Dawkins (1979) a relatedness of 0.8 should not only indicate that 80% of two individuals' genes are identical, but that they are also identical by descent (Malécot, 1969), meaning that they come from a common ancestor. However this approach also runs into problems as identified by Seger (1981) in that, if it is assumed that each mutation produces a new gene, then all identical genes in the population share this new gene as a common ancestor at some point in their history. Grafen also identified that Hamilton's rule does not take account of the details of the genetic representation of the altruistic trait, such as ploidy and dominance or

recessiveness. In an attempt to answer these problems Grafen presented a method of geometrically visualising relatedness, as well as a corresponding algebraic method, valid for different genetic representations. Additionally Grafen (1985b), commenting on Queller's (1985) derivation of Hamilton's rule, noted that it is in fact the actual degree of genetic similarity that is significant for Hamilton's rule, irrespective of whether that genetic similarity is caused by common ancestry, association of individuals with similar genotypes, or some other mechanism.

Pedone & Parisi (1997) have argued that the altruism observable in social groups is not dependent on relatedness, but on homogeneity of behaviour which can be caused by relatedness. They claimed that cultural mechanisms for maintaining behavioural homogeneity could maintain altruism and prevent exploitation. However the existence of such cultural mechanisms is in many cases questionable, and in particular Pedone & Parisi did not explicitly address the problem of invasion of altruistic groups by non-altruistic "mutants".

Engels (1983) took an alternative approach to that commonly used in investigations into kin selection, allowing the cost / benefit ratio, at which individuals behave altruistically to relatives of a certain degree of relatedness, to evolve. Engels' finding was that the equilibrium cost / benefit ratio that actually resulted was half that predicted by Hamilton's rule. Engels concluded that the only way to recover the cost / benefit ratio predicted by Hamilton's rule was to modify the model so that each individual was only presented with the choice to behave altruistically or not.

Queller (1984) combined inclusive fitness theory with game theory to present a formulation of Hamilton's rule that dealt with frequency-dependent effects. Queller showed that interaction between relatives comprised two kinds of fitness effects; inclusive fitness and a frequency dependent "synergistic" effect arising when an individual's behaviour has different effects on interactants depending on whether they perform the same behaviour or not. Queller argued that the frequency dependent effect, being independent of relatedness, should be considered separately to kin selection, and presented a game theoretical treatment of Hamilton's rule which allowed the direction of selection on altruistic behaviour to be determined. Queller concluded that Hamilton's rule is fundamentally correct for describing kin selection, and most deviations from it are due to the separate "synergistic" effect.

Subsequent work by Queller (1992b) answered criticisms of insufficient exactitude or generality in Hamilton's rule, by identifying these criticisms as being due to an interpretation of the costs and benefits of altruism in terms of phenotypes. Queller presented a reformulation of Hamilton's rule interpreting costs and benefits as effects of genes, which he claimed maintained the generality and simplicity of Hamilton's rule.

Watson (1996) suggested that kin selection theory may be applied to the design of cooperative computer systems, and identified the need for standard genetic algorithm and genetic programming approaches to be modified to provide feedback from encoded behaviour into the fitness of "relatives".

1.4.2 Population Genetical Approaches to Kin Selection

Hamilton's inclusive fitness rule has been classified as a heuristic, and therefore insufficiently rigorous for detailed investigations into the evolution of altruism (Levitt, 1975; Cavalli-Sforza & Feldman, 1978;

Feldman & Cavalli-Sforza, 1981; Michod & Hamilton, 1980). More rigorous approaches using population genetics have been presented. Boyd & Richerson (1980) studied the mean equilibrium of quantitative phenotypic characters and determined that the equilibrium was well predicted by Hamilton's rule when selection was weak, but that when selection was strong the mean equilibrium depended on the heritability of the character, with low heritability leading to substantially more altruism than predicted by Hamilton's rule.

Levitt (1975) presented population genetical models of kin selection between siblings under various genetic mechanisms, analysed them for the stability of altruist and non-altruist fixation, and compared them with the predictions made by Hamilton's rule. Levitt concluded that the population genetics approach revealed details of the evolution of altruism under different genetic schemes that are not revealed by Hamilton's rule alone.

Feldman & Cavalli-Sforza (1978) used a population genetic approach to kin selection to show circumstances under which Hamilton's rule did not hold, including non-additivity of fitness costs and benefits. In answering Maynard Smith's (1980) criticisms of their model, Cavalli-Sforza & Feldman (1981) concluded that careful specification of the underlying genetic model was lacking from most investigations into kin selection. The result of this was a body of theory based on gene frequencies rather than genotype frequencies, which was incorrect as genotype frequencies were the quantities of interest, yet these could not be derived from gene frequencies as Hardy-Weinberg conditions did not hold.

Michod & Hamilton (1980) surveyed the different population genetical reformulations of the coefficient of relationship ***r*** used in Hamilton's rule, and concluded that all the reformulations were actually equivalent.

1.4.3 Forces Opposing Kin Selection

When considering kin selection as a potential explanation for cooperative behaviour, it is important to note the possible existence of mechanisms counteracting its operation. Such a counteracting mechanism could exist in the form of competition between relatives for finite resources. Hamilton (1964a) was aware of the potential for populations subdivided into fixed size subpopulations with fixed reproductive potential to inhibit the spread of an altruistic gene, crediting the original discovery to Haldane's (1924) work on competition between siblings. West Eberhard (1975) noted it should be the case that "*the greater the intensity of reproductive or ecological competition between two individuals, the less the probability of altruism between them*", and Grafen (1984) also identified the potential for selection against altruism in sub-divided populations. In his mathematical investigation into the effects of density-dependent mortality on kin selection, Boyd (1982) concluded that if mortality increased with local population size, the relatedness threshold at which individuals were expected to act altruistically towards relatives increased in proportion to the degree of mortality, whereas individuals were expected to harm other individuals with a lower degree of relatedness than this threshold. However Boyd's model was subject to several assumptions, including full mixing of the population at every generation, fixed initial local group sizes, and non-overlapping generations. Wilson et al (1992) studied a viscous population model through computer simulation and concluded that the effects of these opposing mechanisms exactly

cancelled each other, reducing evolutionary fitness to the simplest form of individual fitness. Taylor (1992a) used mathematical models to conclude the same for homogenous environments, as well as extending their results to patch-structured populations (Taylor, 1992b). Taylor (1992b) and Queller (1994) reformulated the measurement of relatedness in such models to show how Hamilton's rule could still give the correct condition for the evolution of altruism. However Kelly (1992a, 1992b, 1994) argued that the areas of interaction and of population regulation need not necessarily coincide as in Wilson et al's (1992) model. Kelly (1992a) presented a mathematical model showing that regulation of a population at the global rather than local level still allowed kin selection to be effective. Kelly (1992b), extending previous work by Boyd (1982), discussed the ecological factors that determine the spatial and temporal scale of density regulation, which include the degree of mobility and the average lifespan of the species undergoing regulation. Kelly (1992b) also suggested that the factors determining the evolutionary fitness of altruism could vary over space or time, which would favour stable polymorphisms of altruists and non-altruists, or plastic phenotypes which could express altruistic behaviour when the ecological circumstances were suitable, such as during periods of low local population regulation pressure.

In addition to identifying different scales of interaction and regulation, kin selection has been suggested to be protected from local density regulation by delays in the effects of regulation on the population (Kelly, 1992b) and by dispersal occurring before local density regulation (Taylor, 1992a; Taylor, 1992b; Kelly, 1994).

1.4.4 Group Selection

Group selection has also been offered as an explanation for the evolution of altruism (Haldane, 1932). In order for group selection to occur, the population must be divided into several groups, within which interactions between members of the group occur. Individuals within these groups are classified as altruists or non-altruists, where altruists give some benefit to other members of their group while incurring a cost, while non-altruists do not, thus receiving the benefits from altruists within their group while incurring no cost themselves. The argument for group selection is that although individual selection will act against altruists within their groups due to the cost of altruism, selection will favour groups containing altruists, either through extinction of groups that do not contain sufficient altruists, or through increased reproduction of groups containing more altruists.

In reviewing group selection models, Maynard Smith (1976) identified the conditions necessary for the establishment and maintenance of altruism under group selection, particularly small group size, low migration rates and rapid extinction of groups containing selfish individuals. Maynard Smith concluded that real populations should be evaluated against these stringent conditions to determine if group selection was likely to have been of evolutionary significance. Echoing Maynard Smith, Rogers' (1990) study into group selection through selective emigration from groups containing more altruists concluded that the one major factor favouring selective emigration was small local group size.

Classical group selection models, such as Wilson's (1975), have been the subject of extensive criticism, which generally focuses on the problem of individual selection exerting a greater pressure than selection at the level of the group. An example of this fundamental problem can be seen in Thompson's (1998)

reply to Wilson & Sober's (1994) argument for a unified theory of natural selection operating on a nested hierarchy of units. As an explanation for how group selection could occur, Thompson presented arithmetic examples in which the frequency of some quantity in a global population, such as altruism, could increase despite decreasing in frequency within the subpopulations comprising that global population. In their response, Wilson & Sober (1998) identified this phenomenon as Simpson's Paradox. However Simpson's Paradox is seemingly only applicable for infinite populations, as proportions within groups cannot decrease indefinitely unless the group size, and hence global population size, can continue to increase indefinitely, otherwise the lowest possible proportion in a finite group is eventually reached in the form of a single member of that group. Hamilton (1963) identified this problem inherent in group selection as described by Haldane (1932), and subsequently Pollock (1983) illustrated it with his computer simulations of between-group selection, in which altruism failed regardless of the costs and benefits involved.

Goodnight (1992) responded to criticisms of classical group selection such as Pollock's (1983) by proposing a "budding-viscous" population model, in which stochastic variation in the formation of daughter groups from reproducing groups led to concentrations of altruists within them, allowing between-group selection to operate. Similarly, Cohen & Eshel (1976) presented a colony model which supported variance among individuals by establishing new colonies from small groups of founders, facilitating the spread of altruism. This model was based on their conclusion that an altruistic trait can only spread in a population if the benefit from an altruistic action is directed to other altruistic individuals more than it is to selfish individuals, which normally requires the local frequency of altruists around the altruistic actor to be greater than the population average. Charlesworth's (1979) investigation of Wilson's (1975) model drew similar conclusions, and showed that altruism could not be favoured in the model unless the altruists also received the benefit of their own altruism, leading Wilson (1979) to argue for the evolutionary importance of such "weakly altruistic" traits.

It has been argued that group selection and kin selection are different forms of the same process. After describing the kind of classical group selection models reviewed by Maynard Smith (1976), Grafen (1984) presented examples of a new form of group selection model based on Hamilton's rule, such as that developed by Wade (1980). Eshel (1982) presented a mathematical model agreeing with Wright's (1945) theory that the evolution of altruism requires a partial separation of the population into relatively small mating populations, known as demes, with a low rate of migration between them. In the course of his investigation, Eshel noted that the distinction between group selection and kin selection in the model was not clear, as a low rate of migration between demes would necessarily increase the rate of identity by descent within them. Similarly Queller (1992a), studying the implications of non-additive fitness effects for inclusive fitness using a quantitative genetic mathematical model to separate phenotypic fitness terms from genetic terms, concluded that inclusive fitness and group selection were different ways of viewing the same selection process, and that neither was more general than the other with regard to non-additive fitness effects. Pepper & Smuts (1999) also presented results from a simulation model suggesting that kin selection is an important component of between-group selection.

As well as the above claims for the identity of kin selection and group selection, arguments have been made for their distinction. Maynard Smith (1976) made one such argument, and identified the distinguishing features of group selection models as being; the requirement for partially isolated reproductive groups, group extinction and group reproduction, whereas for kin selection the distinguishing feature is proximity of relatives in order for actions to effect relatives' reproductive fitness. Similarly, Dawkins (1979) included "kin selection is a form of group selection" as one of the twelve misunderstandings of kin selection. Dawkins showed this to be incorrect by noting that kin selection can occur in any population where individuals are statistically likely to encounter relatives, without the need for discrete groups within the population.

As has been shown in this section, group selection is an area of continuing controversy. However, the questions of whether or not classical group selection is possible in real populations, whether it supports only kinds of altruism that directly benefit the altruist, and whether kin selection and group selection are best viewed as different forms of the same process, do not impact on the use of Hamilton's rule to determine if altruism should be favoured between related individuals, which shall be the approach used in this thesis.

1.4.5 Memic Evolution

Evolution is usually considered to act via genetic transmission of useful traits. However Dawkins (1976) has proposed a mechanism of cultural transmission of traits, known as memic evolution. In genetic evolution the unit of replication is the gene, which has a physical basis, whereas in memic evolution the unit of replication is the meme, which is an idea or concept contained in the mind of an individual. While genes are, with some exceptions, transmitted to offspring through reproduction, memes spread in a population through mechanisms such as learning and imitation. Dawkins argued that cultural evolution is now more significant for human society than genetic evolution, as it can proceed much more quickly. This is because genetic evolution is dependent on the maximum reproductive rate of a species, which is perhaps one offspring per year in the case of humans, whereas memic evolution depends only on the speed with which learning and imitation can occur, which is many orders of magnitude faster. Many genetic models can also be interpreted as memic models. For example, a model for the spread of cooperation may be based on cooperation under genetic control, while also being valid for cooperation under memic control.

1.5 Motivation and Aims

As has been described above, there appear to be two mechanisms that can lead to the evolution of cooperative behaviour in populations of self-interested individuals; repeated interaction and kin selection. As will be described in the next chapter, the study of these two mechanisms has previously been carried out in isolation. However the study of these mechanisms in conjunction is interesting, as kin-selected altruism has been suggested as a possible precursor to the evolution of reciprocal cooperation (Axelrod & Hamilton, 1981). Trivers (1971) has also noted that kin selection and reciprocal cooperation are favoured under the same conditions and are therefore difficult to discriminate between, as well as noting that the

two mechanisms can occur in parallel and interact in interesting ways. Trivers argued that the interaction between kin selection and reciprocal cooperation could have been significant in human evolution. This thesis shall therefore aim to design a model that supports both the evolution of cooperation through repeated interaction and through kin selection. The thesis will present a theoretical investigation of the behaviour of the model and the roles of these two mechanisms in explaining any cooperation observed in the model, as well as an investigation of the ways in which they interact together, with the hope of gaining a greater understanding of the operation of these mechanisms and the circumstances that favour them.

1.6 Conclusion

This chapter has introduced the fields that this thesis draws upon; Artificial Intelligence, Artificial Life, game theory and theoretical biology. The Prisoner's Dilemma has been introduced, as well as other 2 x 2 games, and the mechanism of repeated interaction proposed as a means of promoting cooperation in populations of self-interested individuals. Kin selection theory has also been introduced as a means of promoting cooperation in populations of self-interested individuals. It has been argued that both of these mechanisms are supported in spatial populations with local interactions among individuals. In the next chapter it shall be shown that while kin-selected altruism has been claimed to lead to reciprocal cooperation, the two mechanisms have not been studied in conjunction, and this shall be taken as the motivation to design a model with the aim of investigating the operation of these mechanisms, their relative importance, the circumstances under which they are favoured, and the way in which they interact. The remainder of this thesis is divided as follows: in chapter 2 previous approaches to the study of cooperation are surveyed, and evaluated where they are relevant to the approach taken in this thesis. In chapter 3 the design of the proposed model is presented and in chapter 4 its implementation is presented. In chapter 5 experimental results collected using the model are presented, and in chapter 6 these results are discussed. Chapter 7 presents the conclusions drawn from the work, and identifies areas of future research.

Chapter 2 – Background

2.1 Introduction

A large literature has developed on cooperation, largely taking the Prisoner's Dilemma (PD) as its model of social interaction. In this chapter theories of, and approaches to studying, cooperative behaviour are summarised. In section 2.2 the approaches considered are broadly divided into four categories: finite state automata approaches, genetic algorithm approaches, spatial approaches, and other approaches. Some approaches incorporate ideas from more than one category, and are arbitrarily included in one relevant category. Special consideration is given in section 2.3 to Axelrod's (1980a, 1980b) tournaments and other repeated interaction models, and in section 2.4 to models that investigate kin selection, including Oliphant's (1994) model.

2.2 Approaches to Studying and Promoting Cooperation

2.2.1 Finite State Automata Approaches

The approaches in this section involve the use of finite state automata to encode interaction strategies. An example finite state automaton is illustrated in figure 2.1 below. In this diagram circles indicate state, the unmarked arrow indicates the start state, marked arrows indicate state transitions caused by an opponent's action of the marked type, and letters inside circles represent automata states specifying an output action.

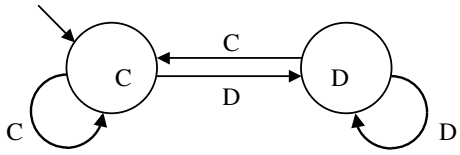

Figure 2.1. A Finite State Automaton for the Strategy Tit-for-Tat

Fogel (1993) used genetic programming to evolve finite state automata to play the iterated Prisoner's Dilemma. Genetic programming uses genetic algorithm style operators (see section 1.2.2) on computer programs in some programming language, rather than on chromosomes. After simulations in which every finite state automaton played every other in a round-robin tournament, it was found that the probability of cooperative behaviour emerging was dependent on variations in the payoff matrix. Three scenarios were identified in which the emergence of cooperation was inevitable, improbable, and apparently random. Fogel suggested that the reward for defection in the Prisoner's Dilemma must be made as small as possible relative to the net gain for mutual cooperation, in order to promote cooperative behaviour. The impact of noisy, or variable payoffs in increasing the evolutionary search time for an optimal strategy was also noted.

Miller (1996) studied a model in which meta-players submitted finite state automata strategies for the repeated Prisoner's Dilemma, and updated their choices using a genetic algorithm. Perfect and imperfect

reporting cases were examined (i.e. noisy and non-noisy). The perfect reporting case meant that players were always informed correctly of their opponent's action, whereas in the imperfect case there was a chance that a cooperation action might be misperceived as a defection action, and vice versa. It was concluded that different levels of noise lead to significant differences among evolving strategies.

Miller et al (1998) studied cooperation in the single-iteration Prisoner's Dilemma, using finite state automata to communicate prior to action choice and subjecting these to evolutionary selection. Contrary to the normal outcome of the single-iteration Prisoner's Dilemma, mutual defection, the model was able to support limited degrees of cooperation. Miller et al studied the dynamics of the system and concluded that the cooperation outbreaks observed were due to transitions in dominance of finite state automata with different communication strategies and different responses to communication.

Banks & Sundaram (1990) studied the structure of Nash equilibria in repeated 2 x 2 games played by finite state automata, taking automata complexity into account. A new criterion of complexity was proposed, accounting for the number of states and transitional structure of a machine. It was discovered that using these preferences for reduced complexity, the set of Nash equilibrium payoffs was drastically reduced, and that the finite state automata always recommended actions that were stage-game equilibria. That is, the actions recommended were always the Nash equilibria for the game in one interaction, such as mutual defection in the case of the Prisoner's Dilemma.

Linster (1992) also studied meta-players choosing finite state automata with complexity considerations, this time in the iterated Prisoner's Dilemma. The focus in this approach was on Nash equilibria and evolutionary stability, and simulations were conducted with replicator dynamics, in which strategies reproduce proportionally to their success in the environment, and mutant strategies do not occur. The results supported earlier claims made by Binmore & Samuelson (1990) for the validity of a type of Mixed Evolutionary Stable Strategy in evolutionary models.

Kirchkamp (1996) considered a spatial environment for the evolution of finite state automata playing 2 x 2 games. Strategies, and rules for learning these strategies from neighbours, were evolved simultaneously. Kirchkamp examined the justification of learning rules as the outcome of evolutionary selection dynamics, and the outcome of using endogenous learning rules, meaning that these rules are not externally specified but arise as a consequence of the model. The conclusion was that endogenous learning rules were less sensitive to changes in sampled neighbours' payoffs and more sensitive to changes in the player's payoff than those previously presented in the literature, however stage-game behaviour was found to be the similar with endogenous learning rules and learning rules takes from the literature.

2.2.2 Genetic Algorithm Approaches

This section details approaches involving genetic algorithms, which were introduced in section 1.2.2.

Axelrod (1987) extended his original work on the Prisoner's Dilemma, which included an ecological tournament using replicator dynamics, to an evolutionary tournament using genetic algorithms. Axelrod's approach was to encode strategies that reacted to three previous Prisoner's Dilemma interactions in choosing their current action. A population of such strategies was then evolved against

eight strategies that were representative of the strategies present in the original ecological tournament. The results showed the establishment of high levels of cooperation through the dominance of Tit-for-Tat-like strategies. Tit-for-Tat is the strategy championed by Axelrod (1984), which begins a Prisoner's Dilemma encounter with cooperation, then reciprocates its opponent's actions, cooperating when its opponent cooperates and defecting when its opponent defects. However, Axelrod's approach has received criticism for its use of a static environment (Miller, 1996). Axelrod did investigate a co-evolutionary environment, but gave little consideration to it, briefly describing an initial dip in cooperation levels, followed by the establishment of high cooperation.

Fujiki & Dickinson (1987) attempted to evolve optimal strategies for the Prisoner's Dilemma, using genetic programming operators to evolve LISP programs. The programs evolved had to interact with a variety of strategies. This approach is similar to Axelrod's (1987), with a different adaptive mechanism, and is therefore subject to the same criticisms of evolution against a static environment.

The dynamics and emergent properties of co-evolving Prisoner's Dilemma strategies were investigated by Hinsch & Merelo (1998), as well as the influence of noise on these dynamics. The genetic operators used allowed strategy genotypes to grow to an arbitrary length, with the aim being to study the effects of infinite memory. It was concluded that cooperation was probable in the long run, even in noisy environments.

Adachi & Matsuo (1992) investigated an ecological model, known as Game World, which evolved automata using genetic algorithms in a spatial environment, with the focus on a variant of the Prisoner's Dilemma. The analysis classified "species" of automata according to strategic tendencies, and examined the varied ecological dynamics of these species.

An alternative approach was taken by Ashlock et al (1996), who studied a model that enlarged on the classical Prisoner's Dilemma by adding the option to choose interaction partners. Again, the model used genetic algorithms to evolve automata. The result found was that the emergence of cooperation in the model was faster with choice and refusal than with a round-robin tournament system, and faster still when compared with a random pairing system. Also, the initial dip in average fitness was much less pronounced. A range of ecologies evolved, from mutually cooperative ecologies to those in which no interaction took place. Social networks of interaction in these ecologies were also studied.

Ikegami (1994), studying genetic programming with simple tree programs for the noisy Prisoner's Dilemma, used a genetic fusion operator that gave rise to the evolution of module strategies that were recombined to form new strategies. Ikegami examined the complexity of the trees in his model, as well as the evolutionary dynamics of the strategies produced. In particular, Ikegami noted that module evolution of strategies, coupled with the large-scale extinctions of strategies observed in his model, could provide conditions suitable for open-ended evolution free of Evolutionary Stable Strategies.

2.2.3 Spatial Approaches

Spatial approaches can vary from pure cellular automata models, in which the states of cells in a grid are updated according to rules acting on their own state and that of neighbouring cells, to models in which the agent population is distributed across a spatial environment, possibly with some degree of movement,

and with local interaction. Frequently the opposite edges of the spatial environment are connected to eliminate the edges, so a one-dimensional environment comes to be shaped like a ring, and a two-dimensional environment comes to be shape like a torus. Figure 2.2 below shows an example Prisoner's Dilemma cellular automata model, which I obtained by implementing a reproduction of Nowak & May's (1993) model, discussed below. In this example each cell represents a single player, with either a pure cooperation or pure defection strategy. Different colours represent different strategy transitions from one time-step to the next as follows: blue indicates a cell that cooperates this round and cooperated last round, red indicates a cell that defects this round and defected last round, green indicates a cell that cooperates this round but defected last round, and yellow indicates a cell that defects this round but cooperated last round.

Hegselmann & Flache (1998) summarised the advantages of using such an approach in modelling social dynamics such as those investigated in this work, which include the potential for; unintended consequences of social actions to arise, qualitative understanding of social mechanisms, models with centralised institutions, exploring consequences of theories, analysing micro-condition effects, and focusing on the dynamics of elementary social interactions. Hassell et al (1991) provided an example of how spatial models can give rise to a wide range of dynamic behaviour, while Durrett (1994) demonstrated the use of cellular automata to give rise to stochastic spatial dynamics observed in different diseases.

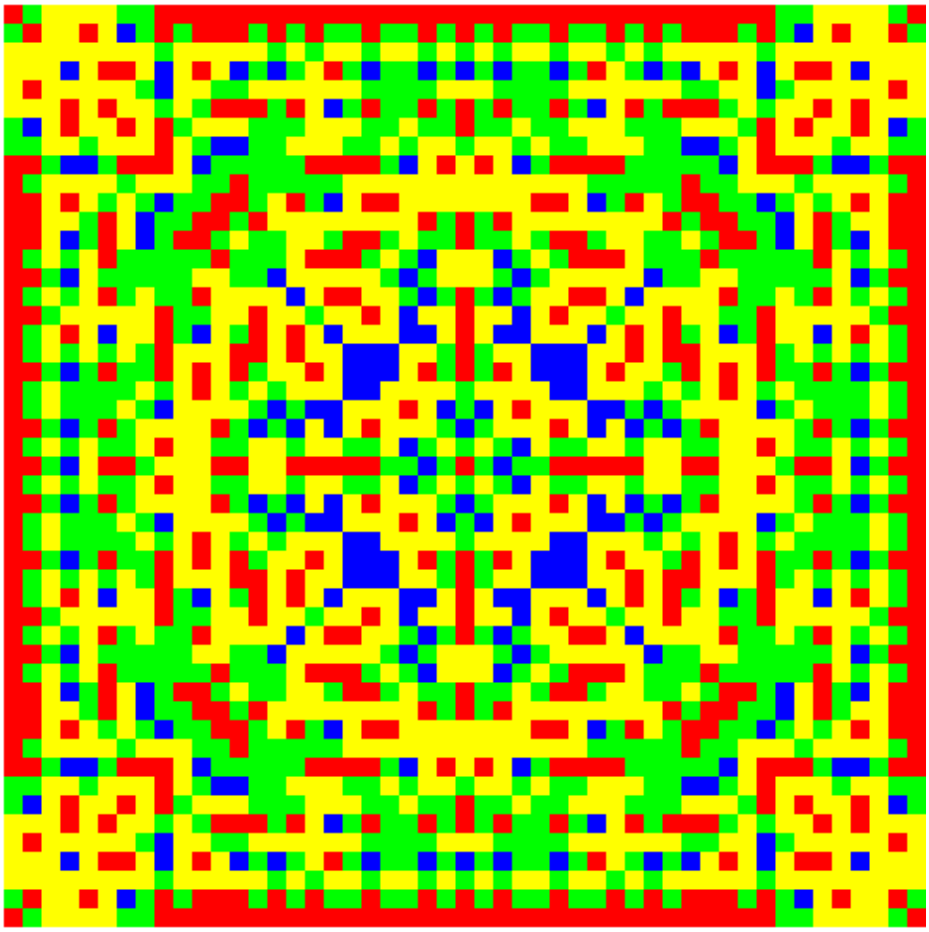

Figure 2.2. Reproduction of Nowak & May's (1993) Prisoner's Dilemma Cellular Automata.

Grim (1997) presented an elegant proof of the undecidability of the Prisoner's Dilemma using a cellular automaton. Grim's proof rests on the fact that Minsky Register Machines are functionally equivalent to Turing Machines and therefore subject to the Halting Problem. Put briefly, the Halting Problem is stated as follows: for a given Turing Machine, which is an abstract computation machine, it is impossible to determine if it will terminate its execution or not. Grim demonstrated that a cellular automaton can be constructed which simulates the operation of any given Minsky Register Machine, and then went on to demonstrate that a form of the Prisoner's Dilemma can be used to represent the rules required by such a cellular automaton. The fundamental result of Grim's proof is that the spatialised Prisoner's Dilemma is subject to Gödelian undecidability. That is to say there is no general method to determine the eventual outcome of inserting a given pattern of strategies into a given background of strategies.

Nowak & May (1992) studied a very simple spatialised Prisoner's Dilemma model, in which strategies and memories were dispensed with to leave two simple types of player, pure cooperators and pure defectors. These players were placed in a two-dimensional environment, where they played the Prisoner's Dilemma with their immediate neighbours. After this interaction, each player adopted the strategy of its highest scoring neighbour. This deterministic local interaction was found to give rise to chaotically changing spatial patterns, with cooperators and defectors both coexisting indefinitely, usually

independently of initial proportions of cooperators and defectors. Nowak & May's findings were criticised by Huberman & Glance (1993) who attributed the spatio-temporal chaos observed in the model to synchronous updating. Huberman & Glance argued that such synchronous updating was very rare in nature and that conclusions drawn on real-world systems from synchronous update models were likely to be incorrect. To illustrate the impact of asynchronous update, they presented an asynchronous version of Nowak & May's model, in which defection came to dominate.

Nowak & May (1993) subsequently extended this work to study additional spatial evolutionary games to the Prisoner's Dilemma, such as Hawk-Dove (see section 1.3.6), while varying parameters such as payoffs, environment sizes and interaction neighbourhoods. The conclusion was that for many evolutionary games, the outcome of frequency dependent selection can be reversed by taking spatial effects into account. The spatial models were also considered as exhibiting aspects of kin selection, reciprocal altruism, and group selection.

Nowak et al (1994) extended this work still further, considering, among others, deterministic versus stochastic rules, discrete versus continuous time, and different geometries of interaction. One of the main conclusions was that spatial effects promote the survival of cooperators, and this conclusion was fundamentally unchanged by such factors as random spatial distribution of players, probabilistic winning, and continuous time. Other factors that favoured cooperators, such as self-interaction, were identified.

An alternative approach was taken by Epstein (1997) who studied mobile players in the Prisoner's Dilemma. Once again, player memories and strategies were not implemented, focusing instead on pure cooperation or defection strategies. In the model presented, players moved and interacted locally with other players. Cooperators and defectors were indistinguishable from each other from the players' view. The results contradicted established views that cooperation cannot persist in the absence of recognition. In fact, the results presented showed that in such an environment, cooperators can dominate the population.

In contrast Mar & St. Denis (1994) investigated more complex spatial models. While the players in their model were static, they were also more complex, having memories and strategies of one or more dimensions (referring to the number of previous interactions used to decide a current cooperate or defect action). Further complexity was introduced in the form of continuous-valued strategies. Prisoner's Dilemma strategies are normally bivalent, that is they specify an explicit cooperate or defect action for a given situation. Continuous-valued strategies, however, specify a probability to cooperate or defect in a given situation. The spatialisation of the model was observed to result in the emergence of continuous-valued strategies more successful than Tit-for-Tat, with certain characteristics such as generosity (the tendency to respond to exploitation with cooperation) and hawkishness (the tendency to respond to a round of mutual defection with further defection).

Similarly Lindgren & Nordahl (1994b) studied 2 x 2 games in an evolutionary spatialised environment. They focused particularly on the Prisoner's Dilemma. Their model allowed strategies to evolve in an unbounded search space through the use of a gene duplication operator to increase the length of strategy

genotypes. Various different spatio-temporal dynamics were observed under varying parameters, which had no equivalent in the non-spatial model. Notably strategies were able to coexist through space-time chaos, and form complex communities through their coexistence in separate spatial regions.

Enquist & Leimar (1993) presented a model in which Prisoner's Dilemma players were mobile within their environment, and hence able to switch partners. It was claimed that such mobility seriously inhibited the evolution of cooperation, by allowing exploitative players to move through a population taking advantage of cooperative players. Investigation of the model showed that the search time for an exploiter to find a new cooperative player was of importance. Also small populations were found to promote cooperative behaviour. As a result of the findings, mechanisms were suggested for promoting cooperation in mobile populations. These included making cooperative players suspicious (tending to defect) at the start of new encounters, and allowing players to "gossip" about other players they encountered, hence providing information about exploiters to be avoided in the population. The ways in which such social controls may be selected for were also considered.

Dugatkin & Wilson (1991) presented a model in which a population is divided into "patches" within which encounters occured at random, proposing this as a way of reconciling repeated interaction with random interaction in the Prisoner's Dilemma. They then introduced a defecting strategy called "ROVER" with the ability to move between patches of cooperators (using the Tit-for-Tat strategy) as it ran out of "naïve" players to exploit. Dugatkin & Wilson showed that a variety of parameter values allowed ROVER to reach fixation in the population, or to reach a stable equilibrium with ROVER as a majority. In addition to considering the assumptions in the model of externally imposed patch structure, and non-mobility of Tit-for-Tat, they also considered ways of modifying Tit-for-Tat to resist defectors, such as refusal to interact, observation of or transmission of information on defectors, and "initiation fees" to join groups of cooperators.

2.2.4 Other Approaches

Numerous other approaches exist, some original, many a hybrid of two or more of the approaches described in sections 2.2.1 to 2.2.3 above. Such approaches are described in this section.

Nash (1953) presented a game theoretic treatment of the case where the participants in a non zero-sum two-person game could communicate to "*discuss the situation and agree on a rational joint plan of action[…] that should be assumed to be enforceable*". Nash's approach was to extend the negotiation process to include the concept of threats.

In contrast, Chantemargue et al (1997) studied a model in which agents were not even aware of the existence of each other, let alone that they were cooperating on a common problem. Chantemargue et al were motivated to examine situations of antagonism, which they claimed were unavoidable in multi-agents systems, yet generally assumed not to occur in the literature. They proposed that such systems need to be sufficiently adaptable to cope with unforeseeable situations, rather than explicitly designing the agents with the capability to resolve antagonistic situations, trading efficiency of solution for reliability, adaptability, scalability and potential for new functions. In their model multiple agents shared a common environment, each sharing the same task of stacking objects found in that environment in a

single location. Antagonism arose because the agents were unaware of each other's existence, and their actions interfered with each other's. Nevertheless such a model did allow the goal to be reached, and Chantemargue et al termed this genuine emergent cooperation, rather than engineered cooperation.

Lindgren & Nordahl (1994a) reviewed approaches to the iterated Prisoner's Dilemma, including some of those listed in this section. In particular they considered the co-evolution of strategies in both universal and spatial games. With the intention of removing constraints and modelling interaction complexity, some Artificial Life extensions to the iterated Prisoner's Dilemma were proposed and implemented, such as artificial ecologies with resource flow and predation. Food webs were also applied to these ecologies, and their community structure studied.

Prechelt (1996) identified several limits of the iterated Prisoner's Dilemma as an interaction model such as binary action choices, fixed and known degrees of cooperativeness for different actions, and interactions that are independent of previous interactions. A new model known as INCA was proposed, which aimed to overcome these limitations. Simulation of the model revealed more complex interaction dynamics than the iterated Prisoner's Dilemma model, and a difficulty in finding simple generally successful strategies.

Axelrod (1986) presented a radically different mechanism for promoting cooperation, known as norms. Norms are rules regarding what is socially acceptable and unacceptable behaviour, and represent a form of self-government. Norms require members of a society to punish those members who do not comply with the society's norms. However, as well as a cost to the punished, such punishment normally involves a smaller cost to the punisher. Axelrod presented the norms game, similar to an *n*-player Prisoner's Dilemma except for the addition of the norms mechanism, and a simulation of this game. The simulation revealed a tendency first for a decrease in the population's willingness to violate a norm, followed by a decrease in the willingness to punish a violation, and finally a resurgence of norm-breaking as a stable state. To counter this, Axelrod introduced the meta-norm concept, in which a failure to punish an observed violation of a norm could be punished by another player who observed both the initial violation, and the subsequent failure to punish. It was found that the norm could become firmly established if the population's willingness to punish norm-breaking was sufficiently high in the first place. Other mechanisms such as dominance of groups or players, internalisation of norms to produce psychological costs for violation, rational consideration of the implications of failure to enforce norms, adoption of behaviours that are wide-spread in a society, membership of a group with a common purpose, the transition of norms into law, and the importance of reputation, were considered as alternative ways to promote norms. Axelrod also considered the possible ways in which norms may be started, in particular through dominance situations, and the importance of reputation. Shoham & Castelfranchi et al (1998) also studied the use of norms, as a method of controlling aggression between agents in a multi-agent environment. The focus of their work was on reducing the costs of compliance with norms, through agent reputations and communication of reputation information between neighbouring agents.

Shoham & Tennenholtz (1992a) presented a method of automatically deriving social laws, which they called the Useful Social Law Problem (USLP). Shoham & Tenenholtz showed that the USLP was NP-complete but under certain restrictions a variant of the ULSP called the Bounded Useful Social Law Problem could be made polynomial. Shoham & Tennenholtz assumed homogenous societies of law-abiding agents in their work, but considered the consequences of relaxing this assumption, speculating that penalties for law-breaking would need to be included in the design process. Subsequently, Shoham & Tennenholtz (1992b) studied the efficiency of evolving social laws in a simulation model.

Nowak & Sigmund (1993a), studying a Prisoner's Dilemma model with a heterogeneous population of simple deterministic strategies, discovered persistent periodic or chaotic oscillations in strategy frequencies and cooperation levels. The strategies considered were two-dimensional, that is they took into account the actions of both a player and its opponent. The interaction model was round-robin, and included noise. Mutation was included to allow the repeated emergence of invading strategies, and this was found to prevent the system from producing an Evolutionary Stable Strategy and instead lead to chaotic oscillations. The addition of Generous Tit-for-Tat, which does not automatically respond to defection with defection, was found to greatly increase cooperation levels in the system. It was concluded that chaotic oscillations seem to be a robust feature of the iterated Prisoner's Dilemma, and that chaos and unpredictability may play important roles in the evolution of cooperation.

Fudenberg & Maskin (1990) conducted mathematical and experimental investigations of noisy repeated games, particularly the Prisoner's Dilemma and the Battle of the Sexes. The basic result of the investigation was the hypothesis that any finitely complex Evolutionary Stable Strategy must give rise to a cooperative equilibrium. A theorem to prove the existence of such a finitely complex Evolutionary Stable Strategy was presented, and some Evolutionary Stable Strategies for the Prisoner's Dilemma and Battle of the Sexes presented. The implication is that although there are cooperative and non-cooperative equilibria in the iterated Prisoner's Dilemma, if an Evolutionary Stable Strategy becomes established, cooperation will arise.

In contrast Eshel & Cavalli-Sforza (1982) argued that both cooperation and defection are Evolutionary Stable Strategies, then studied the problem of how cooperation can become established given this fact. In doing this, they identified the implicit assumption of randomness of encounters when determining Evolutionary Stable Strategies. Eshel & Cavalli-Sforza argued that such random encounters were unrealistic in most natural populations, due to family, population and social structures. They then went on to argue that assortative encounters favour the evolution of cooperation, and that in some cases cooperativeness and assortative behaviour may be co-selected. Of particular interest was their claim that some results of classical kin selection can be explained in terms of Evolutionary Stable Strategies and assortative meetings. Also interesting was a result of the mathematical investigation that concluded that a cooperative strategy would be successful only if the expected number of encounters per individual exceeds some critical value. Eshel & Cavalli-Sforza noted that this result is the opposite of the result from most group selection models, such as that presented by Wilson (1975).

Boyd (1989) introduced implementation mistakes into the repeated Prisoner's Dilemma and discovered that pure strategies (those that are entirely determined by their interaction history) could be evolutionarily stable if they were "strong perfect equilibria" against themselves. Here "strong perfect equilibrium" means a strategy is the uniquely best reply to itself, so that there is no other strategy that performs better against the best reply strategy than it does against itself. In this model, Boyd discovered unconditional and reciprocating strategies, namely pure defection and contrite Tit-for-Tat, which were evolutionarily stable given sufficiently low frequencies of invaders.

Young & Foster (1991) also considered noisy interaction in the iterated Prisoner's Dilemma, however in this case the noise was in the form of variable length Prisoner's Dilemma engagements. In this respect, then, the model presented was similar to many which were not considered to model noise. The model also allowed mutation to introduce new strategies, or reintroduce old strategies into the population. This model was used to plot evolutionary paths, which could be used to determine probabilities for certain strategy distributions in the population, given an initial population state. Young & Foster claimed that noise could drastically change the long-run dynamics of a system, and that the smaller the noise, the larger the change could be. They concluded with the observation that unless cooperative strategies are constantly tested by non-cooperative strategies, cooperation is viable only in the short-term, and not in the long-term.

Sandholm & Crites (1996) studied a reinforcement-learning algorithm known as Q-learning in the context of the iterated Prisoner's Dilemma. Reinforcement-learning is based on the principle that rewarding behaviour should be reinforced in an agent. The interaction between a Q-learner and Tit-for-Tat was investigated, as well as interactions between two Q-learners. Although Q-learners learned to play optimally against Tit-for-Tat, learning the best strategy to play against another Q-learner was found to be a harder problem. This situation could be considered as a form of co-evolution. To this end a series of experiments in simultaneous learning revealed which characteristics of the Q-learning algorithm could be varied to increase performance, although clear cooperation seldom emerged.

Orbell et al (1996) investigated the evolutionary fitness of different methods by which Prisoner's Dilemma players may make predictions about the intentions of their opponent. Two possible mechanisms were considered, cognitively simple projection of the player's intentions onto the opponent, or a more costly ability to perceive the opponent's intentions accurately. Simulations of this model were conducted, which revealed that the projection mechanism was generally successful, and could give rise to a cooperative population, or invade a cooperative perceptive population, given the right conditions. Consideration was also given to the possibility of an evolutionary arms race between the ability to perceive an opponent's intentions, and the ability to hide true intentions from an opponent.

Di Paolo (2000) presented continuous and discrete models of the evolution of altruism under ecological constraints. Di Paolo's model incorporated inverse-density dependent effects, in the form of a requirement for individuals to interact with each other to survive, with density dependent effects, in the form of competition between individuals for finite local resources. Di Paolo observed that there were

qualitative differences between the continuous and discrete models, and concluded that altruism was favoured in the model by a combination of ecological factors and discreteness.

Hemelrijk (1997) presented a computer model which gave rise to individual behaviour which could be explained in terms of game theory, in particular strategies for the Prisoner's Dilemma such as Tit-for-Tat. Hemelrijk's individuals, however, were not programmed to know about the Prisoner's Dilemma, precluding their use of the Tit-for-Tat strategy. Hemelrijk demonstrated with this model that behaviour that could be interpreted as based on game-theory could arise from much simpler rules, and so questioned the explanatory value of game theory for animal populations, and warned against the dangers of misinterpreting and anthropomorphising animal behaviour.

2.3 Axelrod's Tournaments and Other Repeated Interaction Models

2.3.1 Axelrod's Tournaments

Axelrod (1980a, 1980b) presented results from two computer tournaments of the Prisoner's Dilemma. Game theorists were invited to submit strategies to the first tournament, while entry to the second tournament was open to anyone. Entrants to the first tournament received the results of a preliminary tournament prior to submitting their strategy. Entrants to the second tournament received the results of the first tournament prior to submitting their strategy, as well as an analysis of the results including three strategies which would have won the first round had they been submitted. Both these tournaments resulted in the dominance of the simplest strategy, Tit-for-Tat, submitted by Anatol Rapoport. Tit-for-Tat also dominated in hypothetical tournaments with different relative frequencies of the representative strategies in the second tournament. Furthermore, Axelrod conducted an ecological simulation with the strategies from the second tournament, in which each strategy's representation in the population increased or decreased from one generation to the next in proportion to its performance. Again, Tit-for-Tat dominated. This prompted Axelrod (1984) to investigate the characteristics required for success in his computer tournaments. Axelrod concluded that Tit-for-Tat was successful because it possessed the following properties:

- Niceness: Tit-for-Tat was never the first to defect. Niceness was significantly correlated with success in both computer tournaments.
- Retaliatory: Tit-for-Tat retaliated to defection immediately with defection.
- Forgiveness: Tit-for-Tat only punished its opponent once for defection, and thereafter returned to cooperation if its opponent did likewise.
- Clarity: Tit-for-Tat was easily recognisable, and once recognised its non-exploitability was easy to appreciate.

Axelrod went on to consider the stability of cooperation against invasion, and the ability of cooperation to invade defection. Axelrod proposed the term "collective stability" to describe the case where an established strategy's score when playing against itself could not be improved upon by an invading

strategy. Hence in the context of the ecological tournament, the original strategy would not be replaced by the invading strategy. Axelrod represented the collective stability of strategy S_e against any possible strategy S_i by the inequality:

$$V\langle S_i \mid S_e \rangle \leq V\langle S_e \mid S_i \rangle$$

where $V\langle S_e \mid S_i \rangle$ is the expected payoff to an individual playing strategy S_e against an individual using strategy S_i. Thus the concept of collective stability is the same as that of Nash equilibrium. Axelrod argued that collective stability implied evolutionary stability, meaning that no rare strategy can invade a collectively stable strategy with random pairings between individuals. Axelrod (1981, 1984) characterised all collectively stable strategies for the Prisoner's Dilemma using his "characterization theorem":

> *"B is a collectively stable strategy if and only if B defects on move n whenever the other player's cumulative score so far is too great, specifically when*
> $V_n\langle A \mid B \rangle > V\langle B \mid B \rangle - w^{n-1}[T + wP/(1-w)]$."

where ***T*** and ***P*** are respectively the temptation and punishment payoffs from the Prisoner's Dilemma, ***w*** is the shadow of the future, and $V_n\langle A \mid B \rangle$ is ***A***'s discounted cumulative score against ***B*** in the rounds before ***n***.

To overcome the problem of the unconditional defection strategy, All-D, being collectively stable, Axelrod proposed the mechanism of clustering. Taking ***p*** to be the proportion of individuals in a population using the new strategy, the average score of an individual using the new strategy is the weighted average of the score the individual receives from interacting with another individual using the new strategy, and the score the individual receives from interacting with an individual using the established strategy, with the weights being ***p*** and 1 – ***p*** respectively. Axelrod showed that the strategies which were able to invade with the smallest clusters (smallest values of ***p***) were those that were "maximally discriminating" where

> "*a strategy is maximally discriminating if it will eventually cooperate even if the other has never cooperated yet, and once it cooperates will never cooperate again with ALL D but will always cooperate with another player using the same strategy as it uses.*"

Tit-for-Tat is an example of a maximally discriminating strategy. Axelrod also showed that although nice strategies such as Tit-for-Tat could invade All-D, if a nice strategy could not be invaded by a single individual using a different strategy, it could not be invaded by clusters of such individuals. Furthermore, Axelrod showed that if a strategy is collectively stable, it is territorially stable, meaning it cannot be invaded by a strategy that clusters due to spatial proximity.

Axelrod's findings strongly supported repeated interaction as a mechanism for supporting cooperative behaviour. Within the Prisoner's Dilemma Axelrod argued for the superiority of a class of strategies that were nice, retaliatory, forgiving and clear, in particular Tit-for-Tat. Based on the results of his investigation, Axelrod proposed several ways to promote mutual cooperation:

- Enlarge the shadow of the future: either through making interactions more durable, or more frequent.
- Change the payoffs: to make defection less attractive.
- Teach individuals to care for each other: potentially through the mechanism of kin selection.
- Teach reciprocity: in particular Tit-for-Tat.
- Improve recognition abilities: thereby allowing interaction histories with individuals to be accurately assessed.

2.3.2 Responses to Axelrod's Tournaments

Boyd & Lorberbaum (1987) criticised Axelrod's (1984) conclusion for the evolutionary stability of reciprocating strategies such as Tit-for-Tat. Axelrod's argument was based on the concept of collective stability. Axelrod argued that collective stability implied evolutionary stability, meaning that no rare strategy can invade a collectively stable strategy with random pairings between individuals. However, Boyd & Lorberbaum proved mathematically that collective stability does not imply evolutionary stability, and that no strategy for the Prisoner's Dilemma that is fully determined by its history up to interaction t is evolutionarily stable if

$$w > \min[(T-R)/(T-P),(P-S)/(R-S)]$$

where `min` evaluates to the lower of the two values in brackets.

In response to Axelrod's (1984) earlier work, Nowak & Sigmund (1990, 1992) proposed a more biologically relevant model, including noise and stochastic strategies. Their finding was that a Tit-for-Tat type strategy, if present in small levels in a population, could act as a catalyst for establishing cooperation within that population. However, this strategy then gave way to the dominance of a Generous Tit-for-Tat type strategy, at which point evolution stopped. The strategy Generous Tit-for-Tat is a variant of Tit-for-Tat that does not unconditionally answer a defection from an opponent with another defection, but rather has some reduced probability of reciprocating defection. Godfray (1992) also criticised Axelrod's results for the superiority of Tit-for-Tat and supported Nowak & Sigmund's findings. However Axelrod (1984) had already anticipated this criticism, stating "*it was easy to find several rules that would have performed substantially better than Tit for Tat in the environment of the tournament. The existence of these rules should serve as a warning against the facile belief that an eye for an eye is necessarily the best strategy.*" Axelrod identified three strategies that would have won the tournament if submitted, among these the strategy Tit-for-Two-Tats, which is identical in spirit to Generous Tit-for-Tat.

Subsequently Nowak & Sigmund (1993b) continued their investigation of a co-evolutionary Prisoner's Dilemma model with stochastic strategies. Their conclusion was a finding for the evolutionary superiority of a strategy know as Pavlov, or Simpleton, which continues its current behaviour while "winning" (receiving the Reward or Temptation payoffs), and changes when it "loses" (receiving the Penalty or Sucker's Payoff).

Grim (1996) extended Nowak & Sigmund's (1990) treatment to a spatialised stochastic Prisoner's Dilemma model. This model favoured the evolution of even more generous strategies than those favoured in Nowak & Sigmund's model.

The impact of error on evolving Prisoner's Dilemma strategies, in the form of misperception and mis-implementation of actions, was also investigated by Bendor et al (1991). To this end, a similar tournament to Axelrod's (1980a, 1980b) original was conducted, but with the addition of noise and the ability for strategies to adjust their cooperation level between 0 and 100. Once again generosity was identified as being a crucial feature of success in the noisy tournament, and to this end average payoff was plotted against "generosity index" for each strategy and a strong correlation found.

Bendor (1993) extended this work with the noisy Prisoner's Dilemma, considering in particular the trade-off in a strategy between being able to cooperate with other cooperators and being open to exploitation by defectors. It was observed that noise could be detrimental to nice strategies (those which do not defect first in the Prisoner's Dilemma) under certain circumstances. However, it was also observed that noise could promote cooperation, by getting untrusting reciprocating strategies cooperating with each other following an action being misperceived as cooperative.

Nachbar (1992) criticised Axelrod's (1984) findings for the fitness of cooperation, attributing them to strategy set restrictions in the original ecological simulation. This restriction was claimed to leave only pure cooperation equilibria in the simulation. Nachbar presented other simulations that converged to pure defection equilibria, in which, however, partial cooperation was shown to be able to continue for long periods of time.

Martinez Coll & Hirshleifer (1991) also investigated the robustness of Axelrod's (1984) findings and identified several flaws, divided into two main types. These were a failure to appreciate the severity of limiting assumptions in the original work, and an incorrect equilibrium concept. Their own work revealed instead "probability clouds" which tend to attract evolutionary paths in environments with two or three available strategies, although these may not be viable as evolutionary equilibrium points.

2.3.3 Other Repeated Interaction Models

Trivers (1971) was among the first to investigate repeated interaction and the possibilities it presented for reciprocal altruism. Trivers considered several possible methods of dispensing altruism, including random dispersal, dispersal to kin, and dispersal by reference to the recipient's altruistic tendencies. Several characteristics of a species that favoured cooperation were also identified, including long lifetime and low dispersal rate (both promoting repeated interactions between the same individuals). Trivers noted that these same conditions also favour kin selection, making it difficult to discriminate between the occurrence of reciprocal altruism and of kin selection. Trivers also noted the potential for kin selection and reciprocal altruism to occur in parallel and for interesting interactions to take place between them, and argued that such interactions had probably been significant in human evolution. To support his theories, Trivers presented several real-world examples of altruistic behaviour, from fishes and birds, to human beings. An explanation of the possible psychological mechanisms underlying human altruism was also proposed.

Axelrod & Dion (1988) continued Axelrod's (1984) earlier work, attempting to generalise it to more diverse situations including *n*-player games, extended choices including exiting the game or ostracising others, variations in the payoffs, and noisy interactions. Consideration was also given to population dynamics and structure. It was discovered that increasing the number of players in an *n*-player Prisoner's Dilemma makes cooperation more difficult. Reducing the shadow of the future was also shown to reduce cooperation levels. However, changes in the interaction choices and model did not disturb the original findings. Increased strategy generosity was suggested to overcome smaller amounts of noise.

The problem of noisy interaction was studied in more depth by Wu & Axelrod (1995). Three possible solutions to noise were suggested, generosity, contrition and a strategy of "win-stay, lose-shift". Generosity, by not retaliating unconditionally to defection by an opponent, can prevent an inadvertent defection by that opponent from setting up a destructive cycle of defection, such as might occur between two Tit-for-Tat players. Contrition modifies reciprocating strategies such as Tit-for-Tat to avoid punishing a defection received after one of their actions has been misperceived or mis-implemented. The strategy of "win-stay, lose-shift", also known as Pavlov (Nowak & Sigmund, 1993b) was also considered. To investigate the relative success of these different mechanisms, a noisy tournament and an ecological simulation were conducted. It was concluded that reciprocity worked even in the presence of noise, through the adoption of either generosity or contrition. Pavlov, however, was not found to be robust in noisy environments.

Chess (1988) presented a system in which strategies for the iterated Prisoner's Dilemma were represented in integer arithmetic, with three available variables: the last action an opponent took, how many times an opponent had defected in the past, and how many times an opponent had cooperated in the past. Chess' investigations of this model revealed similar dynamics to Axelrod (1987) and Fujiki & Dickinson (1987). However it was observed in particular that it was not important for strategies to be "forgiving" (Axelrod, 1984) in the model. In other words it was not important to try and restore cooperation after a defection by an opponent.

Feldman & Thomas (1987) studied variants of the iterated Prisoner's Dilemma in which the probability of continuing an interaction could be based on either the player's own previous action, or its opponent's previous action. They discovered that if the probability was based on the player's previous action then cooperative strategies could increase when rare in populations of egoists, and also stable polymorphisms could result in the population involving strategies other than just Tit-for-Tat and All-D. Feldman & Thomas also investigated Axelrod's (1984) suggestion of clustering among like strategies and found this could favour Tit-for-Tat's initial increase when rare, and lead to a polymorphic equilibrium with Tit-for-Tat and All-D.

2.4 Kin Selection Models

2.4.1 Oliphant's Kin Selection Model

Oliphant (1994) presented a spatial model of cooperation using genetic algorithms. Oliphant's aim was to demonstrate that the iterated Prisoner's Dilemma was not necessary to promote cooperation, and that in

fact the single-shot Prisoner's Dilemma could give rise to cooperation through the use of a spatial approach with locality of interactions. In fact Axelrod (1984) had already shown this. Oliphant was inspired by Nowak & May's (1992, 1993) spatial models, and to avoid the criticisms of synchronous updating raised by Huberman & Glance (1993) used an asynchronous update mechanism. The model presented was based on a one-dimensional wrap around space, with selection of partners for interaction based on a Gaussian distribution around the individual's site, and distribution of offspring based on the same Guassian distribution. Oliphant presented results from the model for Axelrod's (1984) standard Prisoner's Dilemma Payoff matrix ($\boldsymbol{T} = 5$, $\boldsymbol{R} = 3$, $\boldsymbol{P} = 1$, $\boldsymbol{S} = 0$), and for a Prisoner's Dilemma payoff matrix less favourable to defectors, which was not in fact a strict Prisoner's Dilemma as it violated the requirement $\boldsymbol{R} > (\boldsymbol{T} + \boldsymbol{S}) / 2$. The cooperator favourable payoff matrix showed cooperation to become stably established within the population, while the standard payoff matrix showed some simulation runs reverting to defection from initial cooperation. Oliphant concluded that researchers should carefully consider their motivation for studying the iterated Prisoner's Dilemma, due to the increased cognitive requirements of recognition and memory, when the spatialised single-iteration Prisoner's Dilemma can support cooperation.

Although Oliphant (1994) did not explicitly consider his model as a kin selection model, it was implied as such. In section 3.1 of the paper, Oliphant stated "*they are, in a sense, benefiting their own genes*" and "*individuals are more related (genetically closer) to those nearer to them*". The implication of these statements is that kin selection theory is being suggested as an explanation of observed cooperation, due to the use of a viscous population, which increases relatedness between interactants. In fact this kin selection interpretation of the model is weak, as it is impossible for a cooperator in the model to altruistically benefit a relative. As individuals have only a one-bit chromosome in Oliphant's model, a relative of a cooperator is, by definition, another cooperator. The payoff received by cooperators interacting with one another is the mutually rewarding payoff $\boldsymbol{R}$, hence the interaction is not one of altruism, but of mutual benefit. Perhaps such an interaction could be termed "weak altruism" (Wilson, 1979) in which the benefit of the altruistic act is also received by the altruist, however the usefulness of doing so is questionable. Rather, Oliphant's model should be considered as one in which cooperation is favoured not by kin selection, but by an increased probability of meeting other cooperators.

2.4.2 Other Kin Selection Models

As noted in section 2.4.1, Oliphant's (1994) work was inspired by Nowak & May (1992, 1993). Like Oliphant, Nowak & May (1993) briefly discussed the interpretation of their spatial model in terms of kin selection. As Nowak & May's model used the single-iteration Prisoner's Dilemma this interpretation is subject to the same problems as those identified in the discussion of Oliphant's model in the preceding section, namely that altruism towards relatives under such an interaction scheme is impossible.

Pepper & Smuts (1999) presented a spatial model in which population structure was imposed by patchy distribution of food resources, and studied the evolution of feeding restraint and alarm calling traits in this model. Pepper & Smuts concluded that patchy food distribution supported the evolution of cooperative traits through increasing the genetic variance between trait groups and through reducing

population mixing, which stabilised trait group membership by decreasing within-group genetic variance, as well as allowing delayed benefits from actions such as feeding restraint to benefit the original actor. They also found that increased within-group variance still allowed "weakly altruistic" traits, which benefit the donor as well as other members of the group, to be selected for, whereas "strongly altruistic" traits, which do not benefit the donor but only benefit the others in the group, were not selected for with increased within-group variance. Pepper & Smuts identified opposing forces on population mobility, in the form of the need for increased mobility to export cooperative individuals from successful groups of cooperators, and the need for reduced mobility to isolate and protect groups of cooperators from invasion by non-cooperators. The model presented enabled this conflict to be resolved without recourse to a discrete mixing phase, as used in other models, due to the choice of agent rules which led to an increase in emigration rates from food patches as cooperator frequency increased.

Nowak & Sigmund (1998) studied a model where dispersal of altruism was by reference to the recipient's altruistic tendencies, which they termed indirect reciprocity. They calculated the evolutionary dynamics of a variety of models based on indirect reciprocity, including a model with incomplete information from which they drew parallels between the conditions for evolutionary stability of indirectly reciprocating strategies and Hamilton's kin selection rule for the success of altruism.

2.5 Conclusion

This chapter has surveyed existing approaches to studying and promoting cooperation in the Prisoner's Dilemma and other similar models. Attention has been given to repeated interaction models, which are reviewed in section 2.3, and kin selection models, which are reviewed in section 2.4. In particular Axelrod's (1980a, 1980b) tournaments and Oliphant's (1994) model have been considered in depth. This chapter has revealed that although models in which repeated interaction is used to promote cooperation have been studied extensively, and models in which kin selection is used to promote cooperation have been studied, albeit less extensively, each of these approaches have previously been considered in isolation. There has been a lack of research investigating models that explicitly support cooperation both through repeated interaction and through kin selection. However Trivers (1971) observed that kin selection and reciprocal cooperation are favoured by the same conditions, making discrimination between them difficult. Trivers also noted that kin selection and reciprocal cooperation can occur in parallel and interact with each other, and that this interaction could have been significant in human evolution. Furthermore kin-selected altruism has been proposed as a preliminary stage in the evolution of reciprocal cooperation (Axelrod & Hamilton, 1981). This is taken as the motivation in the next chapter to design a model that supports cooperation both through repeated interaction and through kin selection, with the aim of developing methods of assessing the relative importance of these two mechanisms within the model, and using these methods to understand the circumstances under which each of these two mechanisms contributes to the evolution of observed cooperation, as well as understanding their interactions. Furthermore, kin selection models using the Prisoner's Dilemma have not been extensively studied, and those that have, such as Oliphant's (1994) have typically not provided scope for kin

selection to act on altruistic traits. The study of kin selection in this way does not coincide with the original aim of the theory, to explain the evolution of altruistic behaviour, and so is not of interest here. This observation has shown the need to design a pure kin selection model for the Prisoner's Dilemma that allows altruism, for comparison with the combined kin selection and reciprocal cooperation model. The next chapter presents the design of these models.

Chapter 3 – Design of Models for the Investigation of Reciprocal Cooperation and Kin Selection

3.1 Introduction

This chapter presents the design of the model studied in this thesis. The previous chapter identified that investigations into cooperation to date have concentrated on either repeated interaction or kin selection as explanations for the success of cooperation. Despite the fact that both repeated interaction and kin selection are supported by the same population characteristics, namely populations with limited mobility and local interactions and mating, also known as viscous populations (Trivers, 1971; Hamilton, 1964a), no investigations have been presented into models which allow both mechanisms to function together. However, the study of these mechanisms in conjunction is interesting, as kin-selected altruism has been suggested as a preliminary stage in the evolution of reciprocal cooperation (Axelrod & Hamilton, 1981). Furthermore the potential for interesting interactions between these two mechanisms has been identified, as well as the difficulty of discriminating between them due to the similar conditions under which they are favoured (Trivers, 1971). The motivation for the design of the model presented in this chapter is therefore to provide for both the operation of reciprocal cooperation and kin selection. This model shall be implemented as an agent-based model, rather than a mathematical model, and the motivation for this is given in section 3.2. The design for this model is presented in section 3.3, however in addition to the study of such a model, it is also necessary to design models which study repeated interaction and kin selection each in isolation, in order to investigate how each mechanism functions in the absence of the other. The design of such models is discussed in sections 3.4 and 3.5 respectively. Section 3.6 presents a note on the particular genetic representation used in the models.

3.2 Motivation for the Agent-Based Modelling Approach

In modelling any complex system at least two different approaches are available: mathematical modelling and agent-based modelling. As its name suggests, mathematical modelling uses mathematical equations to capture the dynamics of the system under investigation. Examples of such models can be found in Eshel (1972), Levitt (1975), Boyd & Richerson (1980), among many others. Agent-based models take a different approach, representing each individual in the system separately and defining behavioural rules for these individuals. Agent-based models use a "bottom-up" approach, meaning that the high-level behaviour of the model arises from the specification of simple low-level rules and their interactions. By contrast, mathematical models can be described as using a "top-down" approach, in that they attempt to explicitly represent the high-level behaviour of interest in their equations. A good example of the agent-based approach can be found in Epstein & Axtell's (1996) Sugarscape model. As noted by Pepper & Smuts (1999) agent-based models have not been used extensively in evolutionary biology.

Several advantages have been claimed for agent-based models over mathematical models. Pepper & Smuts (1999) criticised mathematical models due to their requirements for simplifying assumptions such as homogenous randomly mixed populations of infinite size, and for assumptions on population structure. Such models raise questions as to the realism of the assumptions made, and therefore the validity of the results produced. In contrast, Pepper & Smuts summarised the advantages of the agent-based approach as including; a more natural method of specifying individual behaviour and interactions, the ability to incorporate variation over space and time, the ability to incorporate nonlinear dynamics, and the ability to generate population structure from simple rules of interaction, thereby removing the need for assumptions about the structure of the population. Taylor & Jefferson (1995) drew similar conclusions on the advantages of agent-based models over mathematical models, as described in section 1.2.

It is desirable that the model to be studied be, as far as possible, free from potentially unrealistic assumptions, in order the make any conclusions drawn from its study as broadly applicable as possible. This suggests that the agent-based modelling approach is most suitable. Additionally, the model to be studied will implement a viscous population. Such a population is potentially more complex than a fully mixing population, and provides scope for local variations in behaviour in addition to variation over time. Therefore the fact that the agent-based approach allows spatial and temporal variation also marks it as the preferred approach for the model under investigation. The agent-based approach also removes the need for population structure to be assumed, which is helpful in that the structure of a viscous population is not well defined, whereas the conditions of limited mobility and local interaction that give rise to it are. Finally, the agent-based approach allows the behaviour of the model to be specified via simple low-level behavioural rules, rather than attempting to specify the high-level behaviour of the model. This will greatly simplify the implementation of the model under investigation.

The above considerations motivate the use of the agent-based approach in the model presented in this chapter.

3.3 The Design of a Model That Supports Kin Selection and Reciprocal Cooperation

In order to design a model that supports the operation of both kin selection and reciprocal cooperation within it, it is necessary to identify conditions under which these mechanisms are both known to operate. Viscous populations have been claimed to satisfy such conditions (Hamilton, 1964a; Trivers, 1971). Viscous populations are populations which inhabit a spatial environment, and whose members have limited mobility coupled with local interactions and breeding. Such populations are qualitatively different to panmictic, or freely mixing, populations. As Trivers (1971) said

> "*Low dispersal rate during all or a significant portion of the lifetime of individuals of a species increases the chance that an individual will interact repeatedly with the same set of neighbours, and other things being equal one should search for instances of reciprocal altruism in such species.*"

Additionally Hamilton (1964a) said

> "*With many natural populations it must happen that an individual forms the centre of an actual local concentration of his relatives which is due to a general inability or disinclination of the organisms to move far from their places of birth. In such a population, which we may provisionally term 'viscous', [kin selection] may apply fairly accurately to genes which affect vagrancy. [...] over a range of different species we would expect to find giving traits commonest and most highly developed in the species with the most viscous populations whereas uninhibited competition should characterize species with the most freely mixing populations.*"

As viscous populations seem to provide the simplest way of supporting kin selection and reciprocal cooperation through the same mechanism, the design of the model under investigation will therefore include a spatial population with limited mobility, and local interactions and mating between individuals. Furthermore, in order to avoid edge effects, a wrap-around space will be used, meaning that opposite edges of the spatial environment are connected so that, for example, the opposite ends of a one-dimensional space are wrapped-around to form a continuous ring.

As described in section 1.4.1, kin selection favours altruism under genetic control when the ratio of cost to benefit of an altruistic act is less than the degree of relatedness between the recipient and the donor, where the degree of relatedness is equivalent to the probability that the recipient also contains the gene for altruism. Therefore, in order for kin selection to operate in a model, altruism must be under genetic control. The simplest way of achieving this in a computer model is to use an evolutionary algorithm such as a genetic algorithm. As the evolution of cooperative behaviour is the quantity of interest in the model under investigation, that model will use genetic algorithms to encode interaction strategies that determine when to cooperate or otherwise.

It is also necessary to ensure, in order for kin selection to operate, that individuals' behaviour can affect the reproductive fitness of others. This condition can be fulfilled by using the payoffs from social interactions as a form of energy and imposing a continuous energy cost for individuals to remain alive in the model. By combining this with random assignment of available reproductive opportunities over time, higher individual energy leads to a longer lifespan, giving more reproductive opportunities and therefore higher reproductive fitness. Therefore behaviour in social interactions will have a direct effect on the reproductive fitness of an individual and those it interacts with. The degree of selection pressure in the model can be varied by changing the energy cost of living in the model, which varies the minimum amount of energy an agent must acquire from its interactions in order to survive and reproduce. For example, an increased energy cost means that only the most socially successful agents will be selected for reproduction.

As identified in section 1.4.3, when investigating kin selection as a mechanism supporting cooperation it is necessary to consider possible forces opposing kin selection, in the form of competition between relatives for limited local resources (West Eberhard, 1975; Boyd, 1982; Wilson et al, 1992; Taylor, 1992a, 1992b; Kelly, 1992a, 1992b, 1994; Queller 1994). Wilson et al (1992) used computer simulations of a viscous population model with local population density regulation to show that kin selection could

not operate under such conditions. Taylor (1992a, 1992b) came to the same conclusion through mathematical investigations. However Kelly (1992a, 1992b, 1994) argued that population regulation and interactions with relatives need not occur over the same areas, and Kelly (1992a) presented a mathematical model showing that if population regulation were on a global rather than local scale, thereby removing the competition for limited local resources, kin selection would still be favoured. The design of the model under investigation will therefore allow for population regulation to be imposed at either a local or global level, to determine the effects of this on the operation of kin selection. Population regulation will take the form of restriction of available reproductive opportunities according to the remaining population capacity, so that the probability of any individual reproducing is inversely proportional to the difference between the current population size and the maximum population size.

Huberman & Glance (1993) criticised Nowak & May's (1992) findings for the evolution of cooperation in a spatial environment as being an artefact of the use of a synchronous mechanism for updating the population. In order to avoid such criticisms, the design of the model under investigation will use an asynchronous update mechanism, which is described in section 4.4.2.

Finally it is necessary to identify a suitable representation for the interactions between individuals in the model. The class of 2 x 2 games provides the simplest representation of interactions between two individuals in which each individual has a choice of two actions. Section 1.3 presented various 2 x 2 games that are interesting as models of social interaction in that they have non-trivial solutions, that is there is no clear mutually optimal solution but rather there is some conflict of interest. Of the 2 x 2 games presented in section 1.3, the Prisoner's Dilemma, Chicken and Hawk-Dove are the games for which effective strategies for cooperation through repeated interaction can most simply be represented. Effective strategies for cooperation in the Battle of the Sexes and Apology require exchange of roles during the course of a repeated interaction to share the payoffs equitably, and therefore require a strategy that takes account of at least the previous two interactions with an opponent. This complicates the study of reciprocal cooperation. By contrast the Prisoner's Dilemma, Chicken and Hawk-Dove need only take account of the previous interaction with an opponent in order to implement an effective strategy. Of the Prisoner's Dilemma, Chicken and Hawk-Dove, the Prisoner's Dilemma has been the subject of the most research, as it is a very good representation of a common social dilemma, the non zero-sum game, in which both players can share in success, rather than one player or another necessarily "winning" the game.

Chicken is similar in some respects to the Prisoner's Dilemma. One difference is that the requirement of the Prisoner's Dilemma

$$R > (T + S)/2$$

does not necessarily hold in Chicken, meaning that a mutually optimal payoff may be received during repeated interaction in Chicken through alternation of roles between players, as well as by coordinating on the same action. Additionally mutual "defection" in Chicken (playing B) leads to the worst outcome, unlike the Prisoner's Dilemma, which means that, again unlike the Prisoner's Dilemma, there is no action choice that yields a higher payoff regardless of the opponent's action. This undermining of

defection as a dominating strategy in Chicken is likely to provide conditions more favourable to cooperation than those provided by the Prisoner's Dilemma. An interesting side effect of the same fact is that in the iterated game of Chicken, reciprocation of defection by an exploited player (one who plays A against their opponent's choice of B) may not be favoured, as it decreases the payoff to the exploited player if the exploiting player keeps the same choice. This is because in Chicken, unlike in the Prisoner's Dilemma, exploitation of one player by the other is a Pareto-equilibrium, as described in section 1.3.3.

The Hawk-Dove game with averaged payoffs is also similar to the Prisoner's Dilemma, under certain circumstances described in section 1.3.6. Hawk-Dove is more usually studied in the context of the evolutionary stability of the hawk and dove strategies (Maynard Smith, 1978; Grafen, 1979), rather than in the context of strategies for repeated interaction.

Given the interesting possibilities present in the Prisoner's Dilemma, as evidenced by its popularity as a subject of research, the design of the model to be investigated in this thesis will use the Prisoner's Dilemma as its model of social interaction. As Hawk-Dove is closely related to the Prisoner's Dilemma there is little motivation to study it as well. Chicken has some interesting differences to the Prisoner's Dilemma in that defection does not dominate cooperation in Chicken, yet reciprocation of defection is not favoured in iterated Chicken. These differences suggest that the Prisoner's Dilemma is superior to Chicken for studying the evolution of reciprocal cooperation, therefore Chicken will not be investigated in the model. However the different method of supporting reciprocal cooperation in the Battle of the Sexes and Apology, namely exchange of roles over time, is sufficiently interesting to motivate the study of at least one of them within the model, in addition to the Prisoner's Dilemma. Section 3.3.1 shall discuss how to implement strategies for reciprocal cooperation in the 2 x 2 games to be studied, while section 3.2.2 will evaluate their support for kin selection.

3.3.1 Reciprocal Cooperation and the Prisoner's Dilemma

In order to provide scope for repeated interaction to give rise to cooperation in the Prisoner's Dilemma it is necessary to study the iterated form of the game (Axelrod, 1984). Within the iterated Prisoner's Dilemma the simplest strategies available are those of unconditional cooperation (All-C) or unconditional defection (All-D). While such strategies have been shown to be capable of giving rise to global cooperation through the invasion of All-D by All-C (e.g. Axelrod, 1984; Nowak & May, 1992), in order to study reciprocation strategies are required which are capable of acting contingent on the history of an interaction with an opponent. The simplest of these are a class of strategies known as one-dimensional strategies (Mar & St. Denis, 1994). A one-dimensional strategy is a strategy that determines its current action based on its opponent's previous action, except in the case of the first interaction with an individual, for which an action is separately specified. The class of one-dimensional strategies contains some interesting strategies, including the ubiquitous Tit-for-Tat (Axlerod, 1984). However, a simple extension to the one-dimensional strategy yields the two-dimensional strategy, which determines its current action based on the combination of its opponent's previous action and its own previous action, again excepting the case of the first interaction with an individual, for which an action is separately specified. The class of two-dimensional strategies, while containing all of the one-dimensional strategies,

also encompasses some more interesting strategies. A good example of an interesting two-dimensional strategy is Pavlov, which Nowak & Sigmund (1993b) found to be superior to Tit-for-Tat in the iterated Prisoner's Dilemma with noise. Pavlov bases its decision to cooperate or defect based on whether it received ***T***, ***R***, ***S*** or ***P*** on its previous interaction, and as the only way to determine the payoff from a 2 x 2 game is to know the actions of both players the simplest form in which Pavlov can be represented is as a two-dimensional strategy. A two-dimensional strategy is also the simplest way to represent an effective strategy for reciprocal cooperation in the Battle of the Sexes or Apology, as discussed in section 3.3.

As shown in table 3.1 below, a one-dimensional strategy has three different variables, each of which can have one of two values. Therefore the class of one-dimensional strategies contains 2^3, or 8 distinct strategies.

Initial action	**C / D**
Action when opponent cooperated on last interaction	**C / D**
Action when opponent defected last interaction	**C / D**

Table 3.1. One-Dimensional Strategy Specification

As shown in table 3.2 below, a two-dimensional strategy has five different variables, each of which can have one of two values. Therefore the class of two-dimensional strategies contains 2^5, or 32 distinct strategies. Table 3.2 presents a classification of each variable of a two-dimensional strategy for the Prisoner's Dilemma according to whether it specifies a cooperate or defect action. These classifications are taken from Mar & St. Denis (1994).

Previous actions agent / opponent	**Cooperation**	**Defection**
Initial action	friendly	suspicious
C / C	constructive	destructive
D / C	merciful	exploitative
C / D	forgiving	vengeful
D / D	dovish	hawkish

Table 3.2. Two-Dimensional Strategy Specification

As the class of two-dimensional strategies both contains more strategies, and contains more strategies of interest than the class of one-dimensional strategies, the two-dimensional strategies shall be chosen as the simplest strategies that are of interest to study in the iterated Prisoner's Dilemma. Additionally the study of reciprocal cooperation in iterated versions of the Battle of the Sexes or Apology will require the use of two-dimensional strategies. In the context of a genetic algorithm, a two-dimensional strategy can be represented as a five-locus genotype, with each locus specifying an action for a unique interaction history as shown in the first column of table 3.2, and having two alleles, one for cooperation and one for defection.

3.3.2 Kin Selection and the Prisoner's Dilemma

As has been identified in section 2.4, Oliphant's (1994) Prisoner's Dilemma model is weak as a model that supports kin selection. This is because it is impossible for a cooperator in Oliphant's model to altruistically benefit a relative. As individuals have only a one-bit chromosome in the model, specifying either unconditional cooperation or defection, a relative of a cooperator is, by definition, another cooperator. The payoff received by cooperators interacting with one another is the mutually rewarding payoff ***R***, hence the interaction is not one of altruism, but of mutual benefit, or at best "weak altruism", in which the benefit of the altruistic act is also received by the altruist. In section 2.4 it was therefore argued that Oliphant's model should be considered as one in which cooperation is favoured not by kin selection, but by an increased probability of meeting other cooperators.

This section describes in more detail the circumstances under which the Prisoner's Dilemma does not provide scope for kin-selected altruism, then describes how kin-selected altruism can be supported in the Prisoner's Dilemma.

In order to study kin selection in the Prisoner's Dilemma, a model must be designed such that the concept of the coefficient of relationship (Hamilton, 1964a) between two individuals has meaning within the model. Oliphant's (1994) approach was to use genetic algorithms, encoding an individual's strategy phenotype onto a single-bit chromosome, thus allowing for the existence of either purely cooperating or purely defecting individuals within the model. As shall be shown in this section, the approach of using genetic algorithms to support kin selection is correct, but the details require careful consideration.

The problem with using the single-iteration Prisoner's Dilemma for the study of kin selection lies in the structure of the payoffs. Table 1.1, showing the Prisoner's Dilemma payoff matrix, is reproduced below.

	C	**D**
C	3,3	0,5
D	5,0	1,1

Table 1.1 Reproduction. Prisoner's Dilemma Payoff Matrix

(note: payoffs to the row player are listed first)

In the single-iteration Prisoner's Dilemma an individual with an unconditional strategy phenotype of pure cooperation or pure defection, based on a single locus genotype as in Oliphant, will find themselves in the situation of either playing another individual who is genetically identical to them, or entirely genetically unrelated to them. Table 3.3 below shows the possible situations in which an individual plays against a genetically identical individual.

Player genotypes	**Payoffs**
C, C	3, 3
D, D	1, 1

Table 3.3. Single-Iteration Prisoner's Dilemma Payoffs Between Relatives

As can be seen, the payoffs to both individuals are identical when relatives play in the single-iteration Prisoner's Dilemma. This fact precludes the possibility of an individual altruistically benefiting a relative

by reducing its own payoff (fitness) to increase its relative's payoff (fitness). The only way in which one individual could be considered to incur a cost in its cooperation with its relative is by forgoing the higher payoff ***T*** from defecting, and instead receiving ***R***, while similarly the relative's fitness is correspondingly increased from ***S*** to ***R***. However this explanation is meaningless in the context of the single-iteration Prisoner's Dilemma, as if the first individual did defect it would actually possess a completely different genotype and therefore be completely unrelated to the second individual. To summarise, kin-selected altruism requires altruistic interactions between relatives, however in the single-iteration Prisoner's Dilemma with single locus genotypes and deterministic alleles specifying pure cooperation or pure defection, such interactions are impossible.

Table 3.4 below shows the payoffs for single-iteration Prisoner's Dilemma interactions between non-relatives. It can be seen that in such interactions there is the possibility for one individual to altruistically benefit the other, specifically by cooperating while the other defects, thereby incurring a cost of $\boldsymbol{R} - \boldsymbol{S}$ and providing a benefit of $\boldsymbol{T} - \boldsymbol{R}$. The only problem with such altruism in the single-iteration Prisoner's Dilemma, in terms of kin selection theory, is that the altruism cannot be directed towards a relative, as identified earlier in this section.

Player genotypes	**Payoffs**
C, D	0, 5
D, C	5, 0

Table 3.4. Single-Iteration Prisoner's Dilemma Payoffs Between Non-Relatives

The only way to overcome the limitation of altruism occurring only between non-relatives, assuming deterministic strategies, is to find some genetic representation that allows interactions of the type shown in table 3.4 above to occur between relatives. This can be achieved if such interactions are controlled by different loci in each of the interacting individuals. Then an allele for cooperation at one locus controlling behaviour for an interaction will be able to altruistically benefit its copy in a related individual, provided that related individual uses an allele for defection at a different locus to specify its behaviour for that interaction. Such a situation cannot arise in the single-iteration Prisoner's Dilemma with single locus deterministic strategies.

Having identified conditions that are necessary to support altruism through kin selection, the next step is to decide on a model that does provide scope for kin-selected altruism. The decision to study two-dimensional strategies, made in section 3.3.1, provides the answer to this decision as well. If individuals play the iterated Prisoner's Dilemma using two-dimensional strategies encoded into their genotypes, then there are two situations in which two individuals will both be using different loci on their genotypes to determine their current action. These situations occur when one individual cooperated on the last turn while the other defected, or vice versa. In such a situation, using the terminology of Mar & St. Denis (1994) presented in table 3.2, one individual will use the locus on their genotype that determines whether they are merciful or exploitative, while the other will use the locus on their genotype that determines whether they are forgiving or vengeful. Therefore according to the criteria defined above, the use of genotypes encoding two-dimensional strategies for the iterated Prisoner's Dilemma provides the

necessary conditions for kin-selected altruism to occur. It should be noted that the requirement for the agents to have chosen opposite actions on their last encounter means that such altruism can only appear in the Prisoner's Dilemma if iterated interaction occurs. It should also be noted that as mutual cooperation can become established without reference to the loci subject to kin selection, mutual cooperation is possible between individuals that are completely unrelated at these loci.

For the iterated versions of the Battle of the Sexes and Apology, benefit to a relative is possible under the same circumstances as the in the Prisoner's Dilemma, namely when each player chose a different action on their previous encounter. However in the Battle of the Sexes and Apology, such benefit is not strictly altruistic, as there is no cost to the donor. This point will be expanded on in section 6.2.1.

If kin selection operates in the model, areas of highly related highly cooperative agents should be observable. In order to visualise this, it is necessary to develop a technique for combining two sets of spatial data into one representation of the environment. These data sets are the level of cooperation among agents in each area of the environment and the relatedness of the agents in each area of the environment. The design of the model for investigation will incorporate such a visualisation technique, which is described in section 4.6.2.

3.4 The Design of a Model That Supports Only Kin Selection

In order to design a model that supports only kin selection, it is necessary to use the single-iteration Prisoner's Dilemma. This is because in order to study only kin selection as an explanation for cooperation it is necessary to eliminate the potential for reciprocal cooperation to occur within the model, which is best achieved by avoiding repeated interaction in the Prisoner's Dilemma. The single-iteration Prisoner's Dilemma can be enforced even in a model in which individuals interact repeatedly, by not allowing individuals in the model to store a memory of the behaviour of other individuals in previous interactions. Oliphant (1994) used the single-iteration Prisoner's Dilemma in his model of kin selection, however as shown in section 3.3.1, Oliphant's model does not support altruistic interactions between relatives, which are essential for altruism to be favoured by kin selection. As described in section 2.5, kin selection is most interesting as an explanation for altruistic behaviour, so a model for the study of kin-selected altruism is required. Here I propose a simple method of allowing altruistic interactions to occur between relatives, by introducing the concept of roles into the basic Prisoner's Dilemma interaction. In each Prisoner's Dilemma interaction a role can be assigned to each player, one player is assigned role 1, which may correspond to being the initiator of the interaction, while the other player is assigned role 2, which may correspond to being invited to interact by the initiating player. Given this role assignment, it is now possible to specify a strategy for the single-iteration Prisoner's Dilemma which is contingent on the role of the player, specifying one action in the Prisoner's Dilemma if the individual is assigned role 1, and another action (possibly the same) in the Prisoner's Dilemma if the individual is assigned role 2. Such a strategy can be encoded on a two locus genotype, with the allele at the first locus specifying the Prisoner's Dilemma action if assigned role 1, and the allele at the second locus specifying the Prisoner's Dilemma action if assigned role 2. As each player in such a Prisoner's Dilemma interaction always has a

different role to the other, each individual's action will be specified by a different locus on their genotype, which is the requirement specified above for kin-selected altruism to be able to occur. Figure 3.1 below illustrates a situation in which an allele for cooperation at the first locus of an individual's genotype can altruistically benefit a copy of itself in an individual with which it is related at that locus, by providing the higher payoff ***T*** to that individual during a single-iteration of the Prisoner's Dilemma.

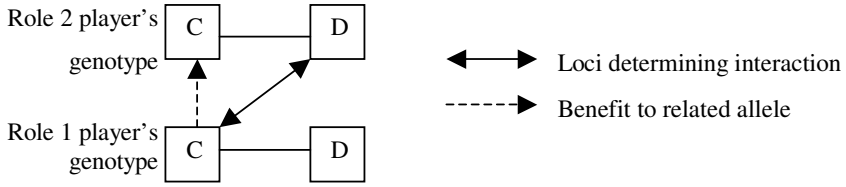

Figure 3.1. Altruistic Benefit To a Relative in the Single-Iteration Prisoner's Dilemma with Roles

An alternative method of allowing altruistic interactions to benefit relatives in the single-iteration Prisoner's Dilemma is to use non-deterministic strategies such as those used by Mar & St. Denis (1994). Such strategies are specified as the probability of cooperating or defecting in a given situation, so for the single-iteration Prisoner's Dilemma a non-deterministic strategy simply specifies the probability of cooperating on each interaction. Non-deterministic strategies provide scope for alleles altruistically to benefit copies of themselves in relatives, because the probabilistic nature of such strategies do not inevitably lead to mutually beneficial cooperation / cooperation interactions between predominantly cooperative individuals, but allow occasional cooperation / defection interactions to occur, in which one of the relatives acts as the altruistic donor and the other as the recipient. As an example, consider a modification to the single-iteration Prisoner's Dilemma in which the choices of cooperation and defection do not specify deterministic cooperation or defection, but rather specify a ninety percent probability of performing the intended action and a ten percent probability of performing the opposite action to that intended. Such stochasticity in implementing a chosen action was labelled misimplementation by Axelrod & Dion (1988). Given such a model, two predominantly cooperative relatives cooperate most of the time and thus receive ***R***, but occasionally one defects, meaning the cooperator is performing an altruistic act benefiting its relative by $\boldsymbol{T} - \boldsymbol{R}$ through its own cost $\boldsymbol{R} - \boldsymbol{S}$. Of course very infrequently both cooperators defect, resulting in the undesirable mutual punishment ***P***.

This section has identified the requirements for a Prisoner's Dilemma model that supports kin-selected altruism without supporting reciprocal cooperation, and proposed two such models, the single-iteration Prisoner's Dilemma with roles, and the non-deterministic single-iteration Prisoner's Dilemma, although other models exist.

The non-deterministic single-iteration Prisoner's Dilemma, while simple, is highly stochastic. The single-iteration Prisoner's Dilemma with roles is, however, simple and more deterministic, and probably represents one of the simplest possible models that support the operation of kin selection for altruism. The single-iteration Prisoner's Dilemma with roles is therefore the interaction model chosen for use in the pure kin selection model studied in this thesis.

3.5 The Design of a Model That Supports Only Reciprocal Cooperation

In designing a model that only provides scope for repeated interaction as a mechanism supporting cooperation, consideration must be given to whether or not the model inadvertently supports kin-selected altruism.

3.5.1 Existing Reciprocal Cooperation Models

Axelrod's (1980a, 1980b, 1984) tournaments and subsequent ecological simulation represent the most comprehensive investigation to date into repeated interaction as a mechanism supporting cooperation. For altruism to be favoured, kin selection theory requires that individuals may increase the reproductive fitness of relatives at a cost to their own fitness (Hamilton; 1964a, 1964b). Clearly, Axelrod's computer tournaments and ecological simulation do not allow for this situation, as there is no common genetic representation of the strategies, therefore the concept of relatedness for some altruistic trait has no meaning. However, Axelrod's (1987) evolutionary simulation does use a common genetic representation for strategies, which reproduce both sexually and asexually. Axelrod studied both a model in which evolution was against a static environment, and a co-evolutionary system. Axelrod's co-evolutionary simulation does provide the necessary conditions, as identified in section 3.3.2 above, for altruistic interactions benefiting relatives, and therefore does support the operation of kin-selected altruism. However Axelrod did not discuss this aspect of the model in his investigation.

3.5.2 Reciprocal Cooperation Without Kin Selection in an Evolutionary Model

As shown in the previous section, care is needed when studying only reciprocal cooperation in an evolutionary model, such as Axelrod's (1987), to avoid providing scope for kin-selected altruism to occur. In fact this presents a substantial challenge. The problem arises because even the simplest conditional strategies for the iterated Prisoner's Dilemma, one-dimensional strategies, provide the conditions described in section 3.3.2 as sufficient for the occurrence of altruism between relatives. This problem is compounded because the very factors that promote cooperation through repeated interaction by increasing interaction length, namely limited mobility and local interaction, also promote the operation of kin selection. The only way in which to reduce, if not eliminate, kin-selected altruism in the model, while preserving the evolutionary nature of the model and the ability of the strategies to cooperate based on repeated interaction, is to break the association between local interaction and local mating, and enforce a global mating pool with random distribution of offspring throughout the entire environment, while maintaining locality of interactions to allow individuals to interact with each other frequently.

3.6 A Note on the Genetic Model Used

The design presented in this chapter has implied the use of the haploid genetic system throughout. The haploid genetic system is the simplest genetic system, with only one allele at each locus. In contrast,

most animals and plants use the diploid genetic system, in which there are two alleles at each locus, while many species of insects use the haplo-diploid genetic system, in which males have haploid chromosomes and females have diploid chromosomes. The diploid genetic system allows for more complexity in the expression of genetic traits, as the expression of that trait is dependent on not one but two alleles. These alleles can either interact additively, or one may be dominant while the other is recessive. Dominant alleles are those that invariably result in the expression of the trait they encode if they are present at the locus, whereas recessive alleles need to be present in a pair at the locus if their trait is to be expressed. This complexity allows for richer evolutionary behaviour, such as the maintenance in the population of recessive alleles that are lethal when expressed, but that confer some advantage if present at the locus in conjunction with the dominant allele. A well-known example of this can be seen in the case of sickle-cell anaemia, which is typically lethal if two sickle-cell anaemia alleles are present, but which gives protection against malaria if only one of the alleles is present.

Despite the widespread use of the haploid genetic system in evolutionary models, it is worth reviewing the validity of this simplification. Grafen (1984) labelled the assumption of haploidy as the "phenotypic gambit". Grafen established that the gambit is rarely true, at least from the point of view of behavioural ecologists whom he was primarily considering. However, Grafen pointed out that while cases such as that of sickle-cell anaemia are particularly vulnerable to the phenotypic gambit, such cases are also likely to be rare. Grafen also argued, pragmatically, that if the phenotypic gambit were to be abandoned then the study of any character would need to be accompanied by a study of the underlying genetics, thus severely limiting the range of characters that could be studied.

While the implications of the assumption of a haploid genetic system should be remembered, such implications are less significant in the context of the model presented here. This is because the model to be investigated is not a model of any real population, such as a behavioural ecologist might use, but rather the model itself is an abstraction and simplification. In this context another simplification in the form of a haploid genetic system is acceptable, and the question becomes not "what are the implications of this simplification?" but rather "what is to be gained by removing the simplification and thus increasing complexity?" In the study of kin selection and reciprocal cooperation, which the model presented here is designed to undertake, such complexity does not contribute to the investigation.

As for the choice of genetic operators to be used in the model, Fogel & Atmar (1990) have questioned the usefulness of such sophisticated genetic operators as crossover and inversion, presenting experimental results on the solution of linear systems of equations that show rapid convergence with only random mutation. Fogel & Atmar identified problems in which crossover leads to poor performance, and concluded with the claim that crossover and inversion are a subset of random mutation, whose applicability is strongly problem dependent, if advantageous at all. However this claim is the opposite of that made by Holland (1975), who argued that the use of the mutation operator alone reduces a genetic algorithm to a form of exhaustive search algorithm, while the use of the more structure-preserving operators, such as crossover, turns the genetic algorithm into a much more powerful search technique

able to utilise the history of its search to direct future searches. With this in mind, the model to be studied shall utilise a crossover operator, in addition to mutation.

3.7 Conclusion

This chapter has presented the design of a model that supports both reciprocal cooperation and kin selection, and has motivated the decisions behind that design. The design presented has the following features:

- A viscous population structure, in which the population inhabits a spatial environment and individuals within the population have limited mobility, as well as locality of interactions and mating with each other.
- Social interaction between individuals using the 2 x 2 games, in particular the Prisoner's Dilemma, with payoffs from the games used as energy, and with a continuous energy cost for living.
- Individuals implementing two-dimensional strategies for the 2 x 2 games, encoded onto five-locus genotypes.
- Genetic algorithms for reproduction of individuals. Random assignment of available reproductive opportunities according to population density, with population density capable of regulation either on a local or global scale.
- Asynchronous updating of the population.

In addition this chapter has presented modifications to the design of the model described above, to study the operation of kin selection for altruism and reciprocal cooperation in isolation. In order to study kin selection for altruism in isolation within the model, the model's design is modified to use the single-iteration Prisoner's Dilemma with roles as the mechanism for social interaction. In order to study reciprocal cooperation in isolation within the model, the model's design is modified to implement mating and distribution of offspring at a global level, while preserving local interactions between individuals.

The next chapter presents the implementation of the model design presented in this chapter. This model will henceforth be known as the Evolutionary Prisoner's Dilemma (EPD).

Chapter 4 – Implementation of the Proposed Models

4.1 Introduction

This chapter presents the implementation of the Evolutionary Prisoner's Dilemma (EPD) (Marshall & Rowe, 2000) and related models, the design of which was presented in chapter 3.

The Evolutionary Prisoner's Dilemma was implemented in Objective C using Swarm version 2.1.1. Swarm is a software development kit intended to help researchers developing agent-based simulation models. To this end Swarm provides mechanisms to control the execution of agents and hierarchies of agents. Swarm also provides graphical tools to easily display the behaviour of simulations, as well as facilitating different methods of experimentation in the model such as real-time interactive or batch processing of experiments. These factors make Swarm particularly suitable for developing Artificial Life models. Further information on Swarm and downloadable versions of the software are available from the Swarm Development Group's website at `http://www.swarm.org`. The Objective C source for the Evolutionary Prisoner's Dilemma is available in appendix B.

In this chapter, where the Prisoner's Dilemma is mentioned, any of the other 2 x 2 games such as Battle of the Sexes may be substituted.

The Evolutionary Prisoner's Dilemma comprises a population of agents, and an environment in which they are situated. The environment is described first.

4.2 Environment Implementation

4.2.1 Evolutionary Prisoner's Dilemma and Pure Kin Selection Models

Section 3.3 identified the need for a spatial environment, with opposite edges connected to avoid edge effects in the model. The design has been implemented using a two-dimensional environment; therefore the environment is a grid of cells, typically with a width and height of 10 cells, with each edge of the grid wrapped around to meet its opposite edge, thus forming a torus. Each cell is capable of housing any number of agents from zero up to the maximum number of agents in the population. Cells are used as the local area of interaction. That is, agents can only play the Prisoner's Dilemma with, and mate with, agents in the cell they currently inhabit. Offspring from agent mating are placed in the same cell as their parents. At each time step, agents are able to move to any of the eight adjacent cells in their Moore neighbourhood with a certain probability. This movement probability determines the viscosity of the population, the effects of which were discussed in section 3.3. In addition to this physical environment, there are nine environmental variables, namely the mutation rate, the parameterised crossover rate, the maximum population the environment can support, the maximum local population a cell can support, the initial population, the death probability, the movement probability, the initial agent energy, and the energy cost for living. These variables are described in sections 4.3 and 4.4.

4.2.2 Pure Reciprocal Cooperation Model

The implementation of the environment for the pure reciprocal cooperation model is as described in the previous section, with the exception that cells only form the local area of interaction for interactions in the Prisoner's Dilemma. That is agents can only play the Prisoner's Dilemma with other agents in the cell they inhabit, however they can mate with any agent in the entire population. Additionally, agents' offspring are distributed randomly anywhere in the entire environment. The motivation for this mechanism of reproduction was given in section 3.5.2.

4.2.3 A Note on the Topology Used

The topology used to implement the spatial environment in the Evolutionary Prisoner's Dilemma is a two-dimensional grid of cells, with opposite edges of the grid connected to form a torus, and with cells linked to those in their Moore neighbourhood. There are several reasons underlying the choice of this topology. Firstly, two-dimensional grids have been extensively used in modelling complex systems, from the first cellular-automata models such as that of von Neumann (1966). This is probably due to their conceptual clarity, and their ease of implementation and representation. With such grids it is common to connect the opposite edges to form a torus. This is done to eliminate edge effects caused by non-periodic boundary conditions, where cells on the edge of the grid do not have as many neighbours as those away from the edges. The choice of linking cells to the immediately adjacent eight cells in their Moore neighbourhood is also common, although there is more choice in this aspect of the model, for example using a von Neumann neighbourhood of four cells, or alternatives such as random symmetric connection of cells to other cells in the environment. Cohen et al (1999) implemented such a neighbourhood scheme with the intention of determining if persistence of neighbour relations alone was significant in evolving cooperation in the Prisoner's Dilemma, or whether other relationships such as neighbours of neighbours had an effect.

Under the neighbourhood and movement schemes implemented in the Evolutionary Prisoner's Dilemma, agent movement is equally likely to any of the cells in the neighbourhood of that agent's current cell. An alternative neighbourhood scheme with unusual properties is produced, however, when the Evolutionary Prisoner's Dilemma environment is reduced to one dimension, as in section 5.8.2. In this case the toroidal nature of the environment means that once an agent moves, it moves to either of it's neighbouring cells with a probability of 0.375 each, but remains in the same cell with a probability of 0.25. The effect of this is to increase the population viscosity for any movement probability when compared to the two-dimensional version of the model.

In their model Cohen et al (1999) experimentally varied the mechanism by which agents interacted with each other and concluded that the important factor in the model was "context preservation", which is more general than two-dimensional spatiality. As agent interactions did not span generations, Cohen et al argued that context preservation supported cooperation in the model by increasing the "shadow of the adaptive future", meaning that the evolutionary dynamics of local strategy frequencies favoured the evolution of cooperative strategies. In the Evolutionary Prisoner's Dilemma, on the other hand, context

preservation increases the standard shadow of the future, as suggested by Trivers (1971), yet the significance of context preservation remains the same.

4.3 Agent Implementation

Each agent is simply defined, having a genotype, an energy level, and a memory of Prisoner's Dilemma interactions with other agents. First the agents' memory shall be described.

4.3.1 Memory Description

Section 3.3.1 required agents to implement two-dimensional strategies for the Prisoner's Dilemma within the Evolutionary Prisoner's Dilemma and pure reciprocal cooperation models. A two-dimensional strategy requires a memory of the actions of an individual and its opponent on their last interaction. Therefore for every opponent that an agent has interacted with during its lifetime the agent remembers both the last actions of itself and its opponent (cooperate (C) or defect (D) in each case). Every agent has a unique identifying number, providing an index for storage and retrieval of interaction histories in the memory. This memory is used to determine the action an agent will take next time it meets the same opponent. The mapping of this interaction history to an action is achieved by the agent's genotype, as described in the next section.

4.3.2 Genotype Description

The agents' genotypes specify characteristics of the agents, and are used during interaction and mating. For the Evolutionary Prisoner's Dilemma and pure reciprocal cooperation models, the genotype must implement a two-dimensional strategy, therefore a five-locus genotype is required. One locus is used to specify an action for each of the four possible combinations of an individual's previous action and its opponent's previous action, and one further locus is required to specify an initial action when a new opponent is encountered and there is no interaction history against them. Each locus has two alleles, a cooperation allele (represented by a "1") and a defection allele (represented by a "0"). Following Mar & St. Denis (1994), such strategies can be classified according to their characteristics, as described in the reproduction of table 3.2 below.

Previous actions agent/opponent	**Cooperation allele**	**Defection allele**
Initial action	friendly	suspicious
C / C	constructive	destructive
D / C	merciful	exploitative
C / D	forgiving	vengeful
D / D	dovish	hawkish

Table 3.2 Reproduction. Two-Dimensional Strategy Specification

For the pure kin selection model, a two-locus genotype is required, with a separate locus specifying a strategy of cooperate or defect for each role in the single-iteration Prisoner's Dilemma with roles, described in section 3.4.

4.3.3 Energy Level Description

Section 3.3 required that individuals in the model be subject to a continuous energy cost in order to remain alive, and that they replenish their energy levels according to the payoffs from social interactions. Accordingly, the agents also have an energy level, initialised at their birth and decreased by a certain amount every time step. Agents die when their energy level reaches zero, and the only way to replenish this energy and thus survive longer is by receiving payoffs from Prisoner's Dilemma interactions with other agents. The payoff matrix used is shown in table 1.1, in section 1.3.1. Thus, with a living cost of 3 units, agents have to achieve mutual cooperation just to maintain their energy level.

4.4 Model Operation

Finally, the operation of the model needs to be described. This is presented in figure 4.1 below.

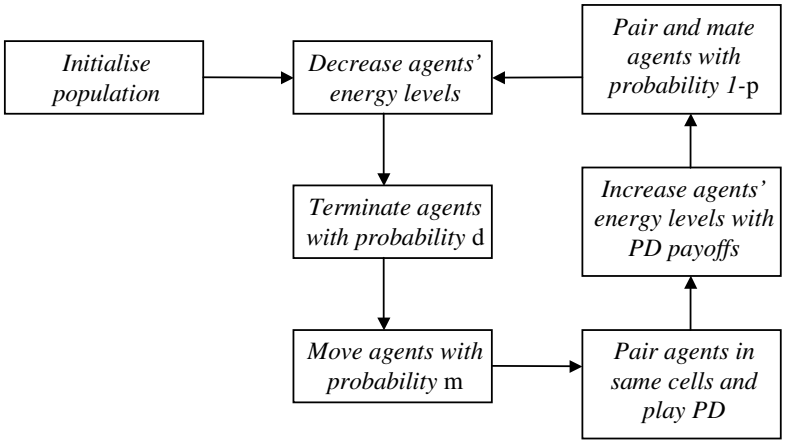

Figure 4.1. The Execution Sequence of the Evolutionary Prisoner's Dilemma

In the first stage an initial population is created, of a size specified by an environmental variable, and randomly distributed over the physical environment. Each agent is given an initial energy level specified by the environment. In the second stage, each agent's energy level is decreased by the living cost specified. Any agent whose energy level reaches zero is removed from the population. The next stage terminates agents randomly according to the probability of death in the environment ***d***. These two methods of termination correspond to "death by starvation" and by "natural causes". In the fourth stage all the agents move with probability ***m*** to a randomly chosen cell in their Moore neighbourhood, which contains the eight immediately adjacent cells reached by moving one cell horizontally, vertically or diagonally in any direction from the cell the agent currently inhabits. This probability can be changed to vary the population viscosity, the implications of which were discussed in section 1.4.1. Next, agents are randomly paired up within each cell, and each pair plays one round of the Prisoner's Dilemma. The action each agent chooses will be determined by their interaction history together, and their individual strategy genotypes. As a result of this, the agents' energy levels are increased in the next stage by the payoff they received from the Prisoner's Dilemma interaction (see table 1.1 in section 1.3.1). Finally the

agents in a cell are again randomly paired up, and produce offspring with a probability $1 - \rho$, where ρ is the proportion of the maximum possible population that the current population represents, and $0 < \rho \leq 1$.

A pair of agents reproduce to combine their genetic material into one offspring agent, whose energy level is initialised to the standard initial energy level. The genetic operators used in the reproduction process are Spears' & DeJong's (1991) parameterised crossover operator, and a standard point mutation operator. The motivation for using these operators was given in section 3.6. Parameterised crossover is a mechanism for combining sections of two parents' genotypes into one offspring genotype. Parameterised crossover was chosen as being less disruptive of effective combinations of alleles than 1-point crossover (Spear's & DeJong, 1991). The process is illustrated in figure 1.2, in section 1.2.2. First, one parent genotype is chosen randomly as the dominant genotype. Then, for each locus, an allele is taken either from the dominant genotype, or with probability χ, from the other parent genotype. Typically χ is set to a low value such as 0.1 (Spear's & DeJong, 1991).

The second operator, point mutation, is intended to reflect replication errors found in biological organisms. For every locus copied during the reproduction process, there is a small probability μ that the allele will be miscopied, which in this case results in a cooperation allele being replaced by a defection allele, and vice versa. Usually μ is set to a very low value such as 0.01. This is similar to the case in natural genetic systems, for example Maynard Smith (1998) estimates that the rate of mutations that produce observable effects is of the order of 10^{-5} in higher animals. Such a low mutation rate may be unsuitable in a genetic algorithm where factors such as small population size may require more frequent mutation to maintain useful diversity in the population.

4.4.1 Update Ordering in the Model

Care needs to be taken in a simulation such as the Evolutionary Prisoner's Dilemma that biases are not introduced into the model due to arbitrarily imposed ordering of execution. For example, if in a simulation the behaviour of simulated components is qualitatively or quantitatively different according to the point within a time-step at which they are updated, and the simulation updates the components in order on a fixed list, then a bias has been introduced to the behaviour of each component based on its position within a potentially arbitrary list.

The Evolutionary Prisoner's Dilemma avoids this problem by randomising the order of updates within the model at each time-step where necessary. In fact, randomised update ordering is implemented only for mating opportunities. The mechanism of interaction in the Evolutionary Prisoner's Dilemma gives each agent in the global population in turn the opportunity to choose an interaction partner in their local cell and engage in one round of the iterated Prisoner's Dilemma with them, unless they have already been engaged for interaction by another agent that round. As each agent chooses a partner at random within their local cell, and each agent can only interact once per round, the ordering of interaction opportunities within the global population has no effect on an agent's chances of interaction. However, the ordering of mating opportunities is significant, as the probability that an agent reproduces is inversely proportional to the population density, therefore those agents allocated mating opportunities first in a time-step will have a higher probability of being permitted to reproduce, while those allocated mating

opportunities later will have lower probabilities of being permitted to reproduce as the agents before them contribute their own offspring to the population, thus increasing the population density. To avoid this effect, the order of matings within the global population is randomised at each time-step.

4.4.2 Asynchronous Updating in the Model

Section 3.3 identified the need to respond to Huberman & Glance's (1993) criticisms of synchronous update mechanisms in spatial models. Huberman & Glance's method of introducing asynchronous update to Nowak & May's (1992) synchronous update model is to subdivide a single time-step in the synchronous model into multiple microsteps. During each microstep at most one individual in the model is updated, while the state of the rest of the model is held constant. It is not clear from Huberman & Glance's description if all other individuals in a population are intended to be updated between updates to the same individual, or whether the asynchronous update mechanism could randomly update some individuals more frequently than others. Assuming the former, which seems reasonable, it is argued that the random update ordering mechanism described in the preceding section implements Huberman & Glance's concept of an asynchronous update mechanism. Certainly this is the only way in which an asynchronous update mechanism can be implemented in the Evolutionary Prisoner's Dilemma. If individuals were to have their complete update sequence as described in figure 4.1 performed in one microstep, then any individual they interacted with in a microstep would necessarily need to be updated also with the payoff from that interaction. Furthermore before this individual could be updated with the interaction payoff, in order to preserve the execution ordering of the model, the individual would need to have their energy level decreased by the living cost and possibly terminated if their energy was fully depleted. If they were terminated another suitable individual for interaction would need to be chosen and updated as just described. This clearly violates Huberman & Glance's requirement that at most one individual be updated in a single microstep, however the situation could be improved somewhat if the update sequence described in figure 4.1 were re-ordered.

In effect then, the Evolutionary Prisoner's Dilemma is divided into three distinct phases, during each of which individuals are updated in microsteps. The first phase determines if individuals are still alive, and gives them the opportunity to move to a neighbouring cell. The second phase allows individuals to engage in interaction with neighbours. The third phase allows individuals to engage in reproduction with neighbours.

4.5 Experimental Configurations

The Evolutionary Prisoner's Dilemma can be compiled in one of two different modes, experimental or observer, by modifying the `Makefile` and the file `EPDDefines.h`. The experimental mode of the Evolutionary Prisoner's Dilemma allows batches of experiments using the model to be performed, with systematic variation of parameters and logging of results. By contrast the observer mode allows real-time examination of the behaviour of the model.

4.5.1 General Model Configuration

The Evolutionary Prisoner's Dilemma allows modification of its model configuration at runtime through editing the data files `payoffs.setup` and `world.setup`. Both these data files are presented in appendix B.

`payoffs.setup` specifies the payoffs used in the 2 x 2 game. It is the user's responsibility to ensure that the payoffs specified satisfy the constraints of the game being used. Only integer values may be specified as payoffs.

`world.setup` specifies the environmental configuration of the model. The parameters that may be specified are; horizontal size of the environment in cells, vertical size of the environment in cells, maximum global agent population, maximum local agent population, initial global agent population, probability of agent death per time-step, probability of agent movement per time-step, point mutation rate, crossover probability, initial agent energy, energy cost per agent per time-step, and the time-step on which to end the simulation.

4.5.2 Experimental Mode Configuration

The configuration of the experimental mode of the Evolutionary Prisoner's Dilemma is possible at runtime by editing the data file `experiment.setup`. This data file is presented in appendix B. `experiment.setup` allows systematic variation of the movement probability in the model, with multiple simulation runs at each movement probability. The parameters that may be specified are; initial movement probability, increment in movement probability, final movement probability, initial simulation run number, and maximum simulation run number.

4.6 Observation

Observation of the behaviour of the model is achieved differently for the experimental and observer modes of the Evolutionary Prisoner's Dilemma.

4.6.1 Measurements of Relatedness

Relatedness is an important variable to quantify when investigating the operation of kin selection. As noted in section 1.4.1, the coefficient of relationship required by Hamilton's rule is the probability that the gene causing altruism on the donor's part is also present in the recipient (Charnov, 1977; Cavalli-Sforza & Feldman, 1978; Harpending, 1979). In real populations it is usually necessary to estimate the coefficient of relationship based on the relatedness of the individuals involved, as determined by their common ancestry, so siblings are traditionally held to have a coefficient of relationship of 1/2 (Hamilton, 1964a). As noted by Grafen (1984), estimating the coefficient of relationship based on common ancestry requires that selection on the trait under investigation is weak. If selection is strong then the coefficient of relationship will be higher than that predicted by common ancestry. However, in a computer simulation of evolution such as the Evolutionary Prisoner's Dilemma, the exact coefficient of relationship between two or more individuals can be determined, for the entire genotype, or for any subset of loci, as described below. This is fortunate as it removes the confusion over how to calculate the coefficient of relationship

from common ancestry, as identified by Grafen (1985a), while also removing the requirement that selection be weak in order for any such calculation to be accurate (Grafen, 1984). It is also fortunate that, for the reasons given in section 3.6, a haploid genetic model is used, as this greatly simplifies the application of Hamilton's rule (Grafen, 1984).

Collins & Jefferson (1991) presented the following formula for calculating the genetic diversity of a group of individuals with two alleles for each locus, where f_i is the frequency of allele 0 (for example) at locus i, l is the number of loci being compared, and $0 \leq D \leq 1$. The relatedness of the same group of individuals is therefore calculated as $1 - D$. A relatedness of 0 indicates a completely unrelated population with a mean distribution of alleles at each of the loci under consideration within the population, while a relatedness of 1 indicates a population that is genetically identical at the loci under consideration. In the Evolutionary Prisoner's Dilemma, individuals have five-locus genotypes, therefore $l = 5$.

$$D = \frac{\sum_{i=1}^{l} (1 - 4(0.5 - f_i)^2)}{l} \tag{1}$$

When considering any two individuals, this operational definition of relatedness quantifies the degree of genetic similarity between them, which in the absence of any information about allele frequencies in the population is equivalent to the probability that both individuals possess any given allele. Hamilton's coefficient of relationship aims to determine the same quantity based on common ancestry. The only difference between these two metrics of relatedness is their accuracy, with relatedness within a simulation being calculable to a higher degree of accuracy and without reliance on assumptions about the strength of selection or the population structure.

Relatedness within the Evolutionary Prisoner's Dilemma can be calculated on different groups of individuals as required. Relatedness can be calculated for the global population, as an average of the internal relatedness of all the local populations in inhabited cells, or as the average of the relatedness between interacting pairs of individuals. Additionally, when calculating relatedness as the average of the relatedness between interacting pairs of individuals, the calculation of relatedness can be limited to only take account of the merciful / exploitative loci and the forgiving / vengeful loci, as these are the loci at which kin-selected altruism can occur. Where relatedness is referred to in the following sections, one of these measures can be used. The choice of which is used is controlled by the header file `EPDDefines.h`.

4.6.2 Visualisation of Kin Selection

Section 3.3.2 identified the need to visualise the operation of kin selection through the development of a technique for combining two sets of spatial data into one representation of the environment. These data sets are the level of cooperation in each cell and the relatedness of the agents in each cell. The level of cooperation is calculated as the proportion of cooperative actions from the total actions within a cell during one time step. The level of relatedness within the cell is calculated as described in section 4.6.1.

Given the cooperation level and relatedness data sets, there are two values in the range 0 to 1 for each cell in the environment. These values are then combined into a single colour value for display, interpreting the values as colour levels in the "Red, Green, Blue" (RGB) colour scheme. By using the cooperation level as the red colour level, the relatedness as the green colour level, and setting the blue colour level arbitrarily to its highest value, the colour descriptions of a cell given in table 4.1 below are obtained.

R, G, B	Colour	Description
1,1,1	White	cooperative & related
0,0,1	Blue	uncooperative & unrelated
1,0,1	Magenta	cooperative & unrelated
0,1,1	Cyan	uncooperative & related

Table 4.1. Colour Descriptions of Cell Populations in Visualisation

The different possible colours for a cell are presented below in figure 4.2 as a colour chart. This chart shows the cell colour over the full range of cooperation and relatedness levels for a cell, with an interval of 0.1 for both levels.

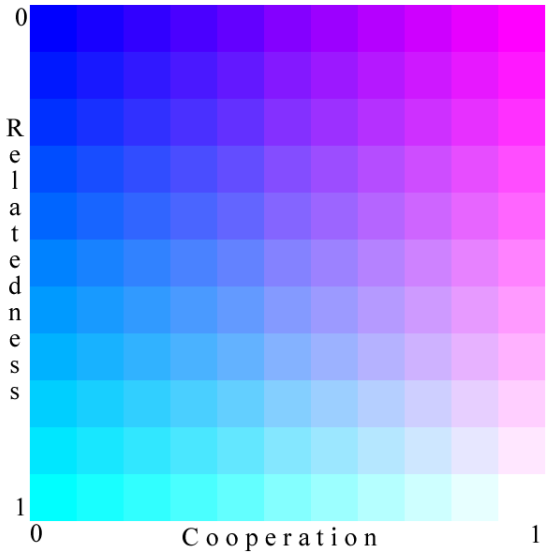

Figure 4.2. Colour Chart for Cell Populations in Visualisation

By drawing these colours onto a grid representing the model's environment, and drawing black for uninhabited cells, it is possible to represent local population cooperation and relatedness. It is therefore possible to visualise the operation of kin selection if it should happen in the model.

A single individual inhabiting a cell will produce a highly related but un-cooperative cell, as it has no potential partners to interact with, but there are also no other individuals to increase the genetic diversity of the cell. In order to distinguish between cells containing single individuals, and cells containing multiple individuals that are highly related but uncooperative, a separate colour is assigned to cells containing only one individual. The colour chosen for this designation is red, as it is sufficiently distinct

from the colours described in table 4.1 above, and from black, which is used to represent uninhabited cells.

A sample visualisation of the relatedness and cooperation in a spatial population is presented in figure 4.3 below.

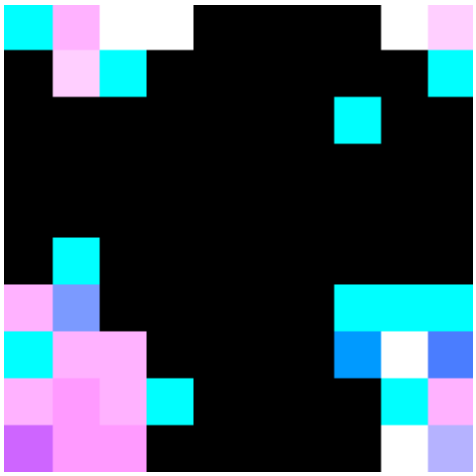

Figure 4.3. A Sample Visualisation of Cooperation and Relatedness in a Spatial Population

4.6.3 Experimental Mode Observation

The experimental mode of the Evolutionary Prisoner's Dilemma logs, for each simulation run, the average percentage of actions during the length of the simulation that were cooperative, the average relatedness over the duration of the simulation, the time-step on which the simulation terminated (to indicate if the simulation terminated early due to population extinction), the average cell population size for inhabited cells over the duration of the simulation, and the average number of distinct partners each individual interacted with over the duration of the simulation. The raw data produced can then be subjected to statistical analysis as required. Formal definitions of the results collected are given in section 5.2.

4.6.4 Observer Mode Observation

The observer mode of the Evolutionary Prisoner's Dilemma presents information on the state of the population, updated in real-time. Appendix C presents a sample of the user interface for the observer mode of the Evolutionary Prisoner's Dilemma.

The percentage levels of cooperation and relatedness between individuals in the population are displayed on a graph, updated in real-time. Additionally, the population size and the frequencies of the five different cooperative alleles in the population gene pool are displayed on another graph, also updated in real-time. As in Mar & St. Denis (1994) these alleles are labelled friendly, constructive, merciful, forgiving and dovish.

A spatial visualisation of the level of cooperation and relatedness within the population using the technique described in section 4.6.2 is also provided, again updated in real-time.

4.7 Conclusion

This chapter has presented the details of the implementation of the Evolutionary Prisoner's Dilemma and its related models. The descriptions of the environment and agents within that environment have been presented. The operation of the model has been described, and has been evaluated against Huberman & Glance's (1993) criticisms of synchronous update models. It has been concluded that the model implements an asynchronous update mechanism as defined by Huberman & Glance. The configuration parameters of the Evolutionary Prisoner's Dilemma and related models have been described. The measurement of relatedness within the model has been defined, and the means by which behaviour in the model can be observed have been presented, including the presentation of a method of visualising the operation of kin selection in a spatial population.

The next chapter presents results obtained from the Evolutionary Prisoner's Dilemma model, the pure kin selection model and the pure reciprocal cooperation model.

Chapter 5 – Results

5.1 Introduction

This chapter presents results collected from experiments carried out using the simulation models described in chapter 4, including the Evolutionary Prisoner's Dilemma and the pure kin selection and pure reciprocal cooperation models. The motivation for the experiments performed was provided in chapter 3. This chapter is divided as follows: section 5.2 formally defines the results collected from the models. Section 5.3 presents results from a control version of the Evolutionary Prisoner's Dilemma in which no selection occurs, section 5.4 presents results from the Evolutionary Prisoner's Dilemma model supporting kin selection and reciprocal cooperation, section 5.5 presents results from the pure kin selection model, section 5.6 presents results from the pure reciprocal cooperation model, section 5.7 presents results from the Evolutionary Prisoner's Dilemma and pure kin selection model using local population regulation instead of global, and section 5.8 presents results from variants on the Evolutionary Prisoner's Dilemma based on Oliphant's (1994) model. Section 5.9 presents results from a variant of the Evolutionary Prisoner's Dilemma with an increased interaction length, and section 5.10 presents results from a study using the Battle of the Sexes payoffs in the Evolutionary Prisoner's Dilemma. Section 5.11 presents visualisations of the population at different movement probabilities, using the technique described in section 4.6.2, for the Evolutionary Prisoner's Dilemma, the pure kin selection model, and the pure reciprocal cooperation model.

Since population viscosity is the quantity of interest for studying both kin selection and reciprocal cooperation, as noted in section 3.3, movement probability in the models was systematically varied in order to collect the results presented here. For all the results 20 simulation runs were performed at each different movement probability, and the results from these simulations were used to calculate the averages and standard deviations shown. Simulations ran to completion unless shown otherwise. Results are not presented for experiments for which they are not relevant, such as average number of interactions for the pure kin selection model. Unless specified otherwise, the payoffs used for all of these results are Prisoner's Dilemma payoffs presented in table 1.1, section 1.3.1: $\boldsymbol{T} = 5$, $\boldsymbol{R} = 3$, $\boldsymbol{P} = 1$, $\boldsymbol{S} = 0$.

5.2 Definition of Results Collected

For each model investigated the results collected were: average cooperation level, average relatedness level, average number of interactions, average run length, average cell population and average lifetime opponents. This section presents formal definitions of the methods used to calculate these results. To facilitate these definitions, the following definitions are provided first:

For all the following definitions, let $k \geq 1$ be the duration of the simulation, and let $\boldsymbol{t}$ be a specific timestep within that simulation, where $1 \leq t \leq k$.

Let A_t be the set of agents in the population that are alive at timestep t, so $A_t = \{a_1,...,a_{s_t}\}$ where s_t is the size of the population at timestep t, and $s_t \geq 1$. Then let $\overline{A}$ be the set of all agents that exist in the entire duration of the simulation, so $\overline{A} = A_1 \cup ... \cup A_k$.

Let Q_t be the set of populated cells at timestep t, so $Q_t = \{q_{t1},...,q_{te_t}\}$ where e_t is the number of populated cells at timestep t, and $e_t \geq 1$. Then let $\overline{Q}$ be the set of all populated cells in the entire duration of the simulation, so $\overline{Q} = Q_1 \cup ... \cup Q_k$.

Let I_t be the set of pairs of agents in the population that interact at timestep t, so $I_t = \{\{a_1,b_1\},...,\{a_n,b_n\}\}$, where $n \geq 1$ unless $|I_t| = 0$, such that for any pair $\{a,b\} \in I_t$, $a \in A_t$, $b \in A_t$, $a \neq b$ and $\{a,b\} \in I_t \Rightarrow \{a,c\} \notin I_t$ iff $b \neq c$. Then let $\overline{I}$ be the set of all pairs of agents that interact in the entire duration of the simulation, so that $\overline{I} = I_1 \cup ... \cup I_k$.

5.2.1 Average Cooperation Level

Average cooperation level was calculated as the percentage of cooperative actions performed by agents in the model out of the total actions performed over the duration of the simulation.

Let c_a be the number of cooperation actions performed by an agent a during its lifetime, and let d_a be the number of defection actions performed by agent a during its lifetime, where $a \in \overline{A}$. So the average cooperation level is

$$\overline{c} = 100 \frac{\sum c_a}{\sum (c_a + d_a)} \forall a \in \overline{A}$$

5.2.2 Average Relatedness Level

Average relatedness was calculated as the average percentile relatedness of all pairs of agents that interacted with each other over the duration of the simulation. This calculation utilises the formula (1) presented in section 4.6.1, measuring relatedness either on all the loci on the agents' genotypes, or only on the loci identified in section 3.3.2 as being subject to kin selection for altruism.

Let D_{ab} be the genetic diversity of the pair of agents {a, b} using formula (1) from section 4.6.1 to measure the genetic diversity of that pair of agents as desired, where l is the number of loci to be compared and f_i is the frequency of a particular allele at locus i among the two agents. Then the average relatedness of the simulation is

$$\overline{r} = 100 \frac{\sum (1 - D_{ab})}{|\overline{I}|} \forall \{a,b\} \in \overline{I}$$

If relatedness is calculated on the entire genotype of the agents, then l is the length of each genotype in the calculation of D, which is 5 in the case of the Evolutionary Prisoner's Dilemma. Let the calculation of average relatedness based on the entire genotype be denoted by $\overline{r_1}$.

If relatedness is calculated only on the loci subject to kin selection for altruism, then in the case of the Evolutionary Prisoner's Dilemma, l is 2 in the calculation of D. The loci considered in the calculation of

D are identified in section 3.3.2. Let the calculation of average relatedness based only on the loci subject to kin selection for altruism be denoted by $\overline{r_2}$.

Unless otherwise stated, each model measures relatedness on pairs of interacting individuals taking account of the full genotype, using relatedness measure $\overline{r_1}$.

5.2.3 Average Number of Interactions

The average number of interactions was calculated as the average number of interactions between all pairs of agents that interacted together at least once over the duration of the simulation.

Let i_{ab} be the total number of interactions between a pair of agents $\{a,b\} \in \overline{I}$. Then the average number of interactions is

$$\bar{i} = \frac{\sum i_{ab}}{\left|\overline{I}\right|} \forall \{a,b\} \in \overline{I}$$

5.2.4 Average Run Length

Average run length was calculated as the average number of timesteps over all simulation runs with the same model configuration, as simulations were terminated early if the agent population became extinct.

5.2.5 Average Cell Population

Average cell population was calculated as the average number of agents in each cell containing one or more agents over the duration of the simulation.

Let p_{tx} be the size of the population at timestep ***t*** in cell $q_{tx} \in \overline{Q}$. Then the average cell population is

$$\overline{p} = \frac{\sum p_{tx}}{\left|\overline{Q}\right|} \forall q_{tx} \in \overline{Q}$$

5.2.6 Average Lifetime Opponents

Average lifetime opponents was calculated as the average number of agents each agent interacted with during their lifetime, over the duration of the simulation.

Let e_{ab} be a pair of interacting agents $\{a,b\} \in \overline{I}$. Then let E_a be the set of pairs of interacting agents which have in common an agent ***a***, so $a \in e_{ab} \forall \{a,b\} \in E_a$ and $E_a \subset \overline{I}$. Then the average number of lifetime opponents is

$$\overline{e} = \frac{\sum \left|E_a\right|}{\left|\overline{A}\right|} \forall a \in \overline{A}$$

5.3 Results from the Evolutionary Prisoner's Dilemma in the Absence of Selection

5.3.1 Description

This section presents results from the Evolutionary Prisoner's Dilemma described in chapter 4, with no selection pressure. These results are presented as control results showing how the model behaves when there is no selection pressure, for comparison with the other results presented in this chapter. The model parameters for these results are presented in table 5.1 below.

Parameter	Value
world size (horizontal)	10
world size (vertical)	10
maximum population	200
initial population	75
death probability	0.05
movement probability	0 to 1
movement probability interval	0.1
mutation rate	0.01
crossover probability	0.1
initial agent energy	15
energy living cost	0
simulation duration	1000

Table 5.1. Model Configuration for the EPD Without Selection

5.3.2. Results

The results from the model are presented in figures 5.1 to 5.4 below.

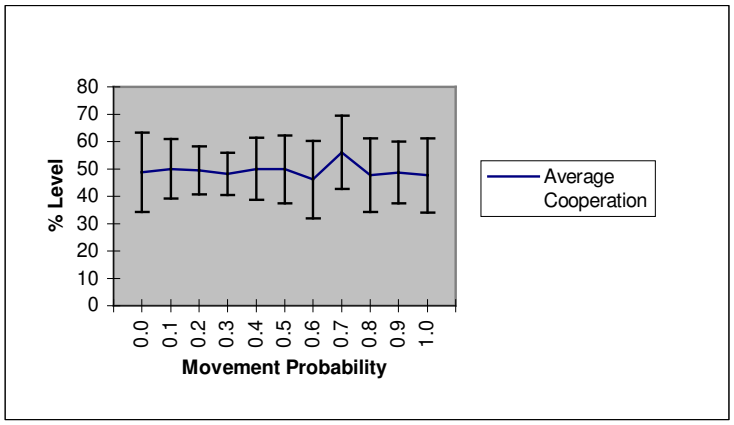

Figure 5.1. Average Cooperation in the EPD Without Selection

Figure 5.1 shows the average cooperation level remaining noisy around the mean as movement probability changes, indicating a lack of selection on cooperation in the model at all movement probabilities.

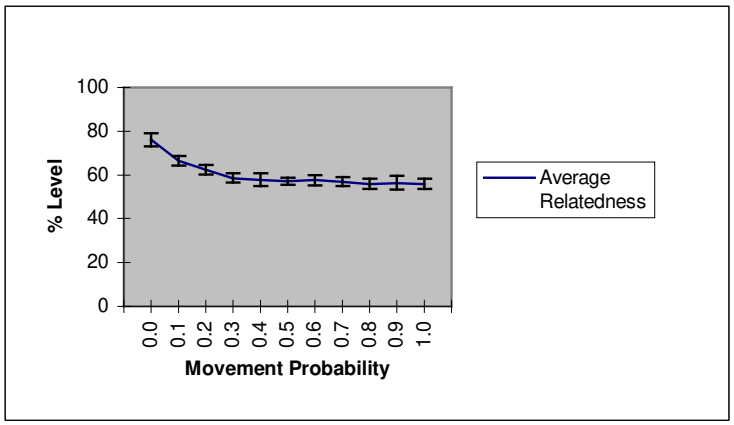

Figure 5.2. Average Relatedness in the EPD Without Selection

Figure 5.2 shows the average relatedness level increasing as the population becomes more viscous, due to decreasing movement probability. This agrees with Hamilton's (1964a) prediction for increased relatedness in viscous populations. Average relatedness is high, at least 60%, across all movement probabilities in the model.

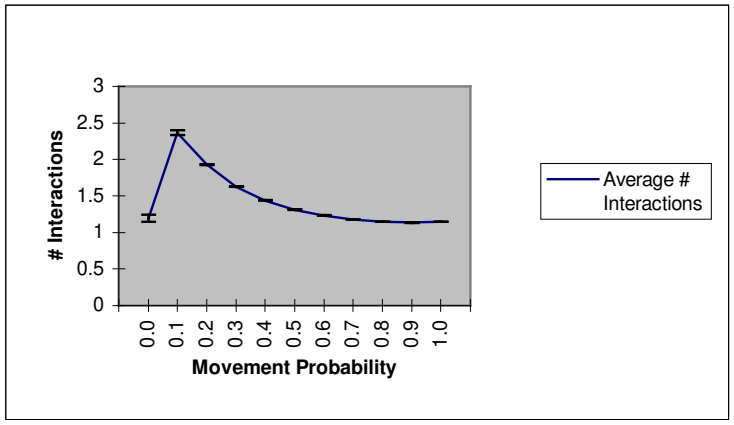

Figure 5.3. Average Number of Interactions in the EPD Without Selection

Figure 5.3 shows the average number of interactions increasing as population viscosity increases, due to reduced movement probability. This agrees with Triver's (1971) prediction for reciprocal altruism to be favoured by viscous populations. However at movement probability 0, the average number of interactions decreases abruptly to just above 1. Note also that the average number of interactions remains low, below 2.5, at all movement probabilities.

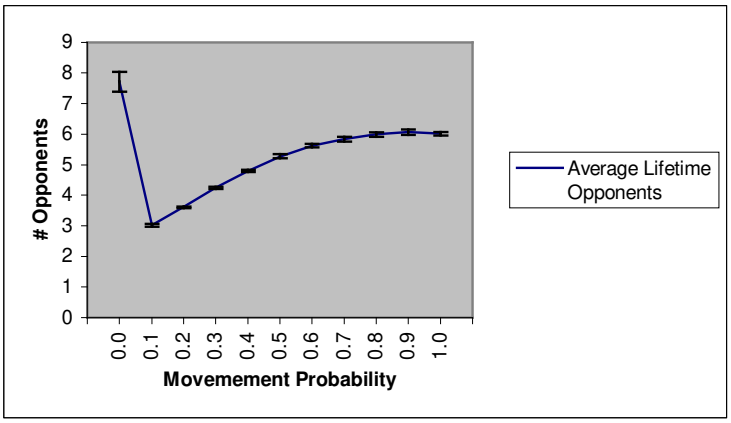

Figure 5.4. Average Lifetime Opponents in the EPD Without Selection

Figure 5.4 shows the average number of lifetime opponents decreasing as the movement probability decreases and hence the population becomes more viscous. However at movement probability 0 the average number of lifetime opponents increases abruptly to its highest level.

5.4 Results from the Evolutionary Prisoner's Dilemma

5.4.1 Description

This section presents results from the Evolutionary Prisoner's Dilemma described in chapter 4. These results were first presented in Marshall & Rowe (2000). As described in section 3.3, the Evolutionary Prisoner's Dilemma provides scope for cooperation both through repeated interaction and kin selection. The model parameters for these results are the same as those presented in table 5.1, with the exception of energy living cost, which increases from 0 to 3 to introduce selection pressure into the model.

5.4.2 Results

The results from the model are presented in figures 5.5 to 5.9 below.

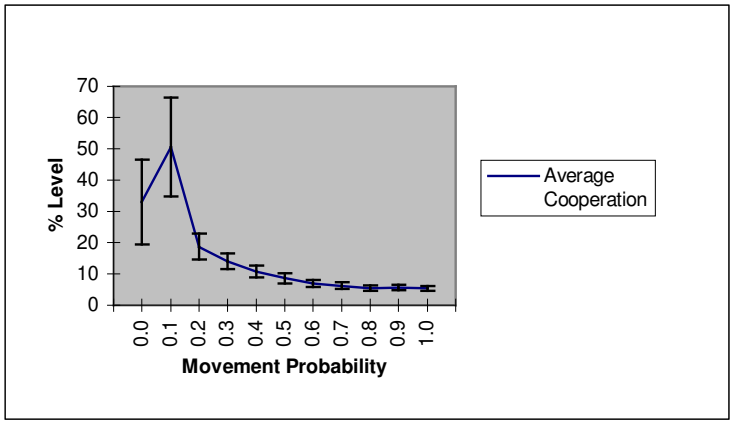

Figure 5.5. Average Cooperation in the EPD

Figure 5.5 shows the average cooperation level at a very low level at movement probability 1, then increasing as movement probability decreases to 0.1. However even at movement probability 0.1, the

cooperation level is only at the mean point, and is somewhat noisy around that point. At movement probability 0 the average cooperation level drops again, while remaining noisy.

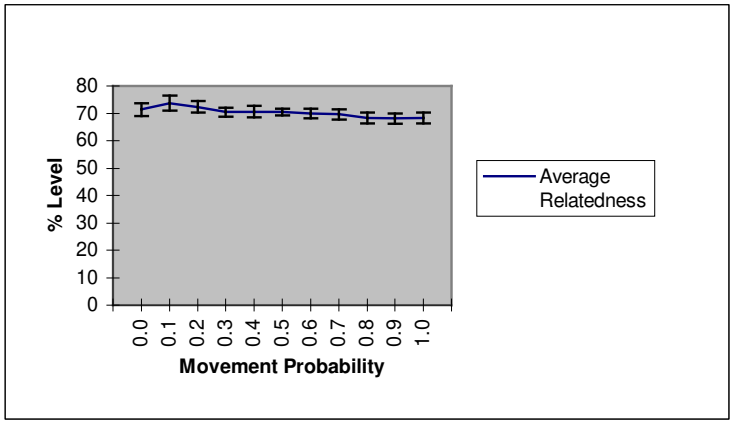

Figure 5.6. Average Relatedness in the EPD

Figure 5.6 shows the average relatedness level, considering the entire genotype. The relatedness level remains consistently high across all movement probabilities, showing little variation.

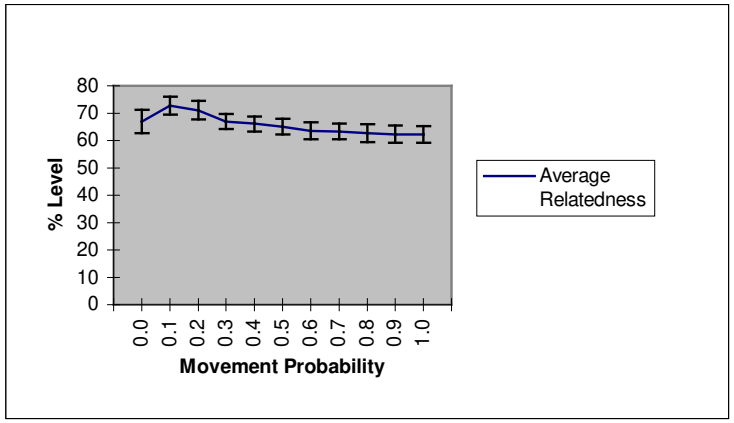

Figure 5.7. Average Relatedness on Loci Subject to Kin Selection in the EPD

Figure 5.7 shows the average relatedness level $\overline{r_2}$, calculated only on the loci subject to kin selection for altruism, namely the merciful / exploitative and forgiving / vengeful loci. As in figure 5.6 relatedness is consistently high across all movement probabilities, however here there is a discernible increase in relatedness as movement probability decreases to 0.1, followed by a drop at movement probability 0.

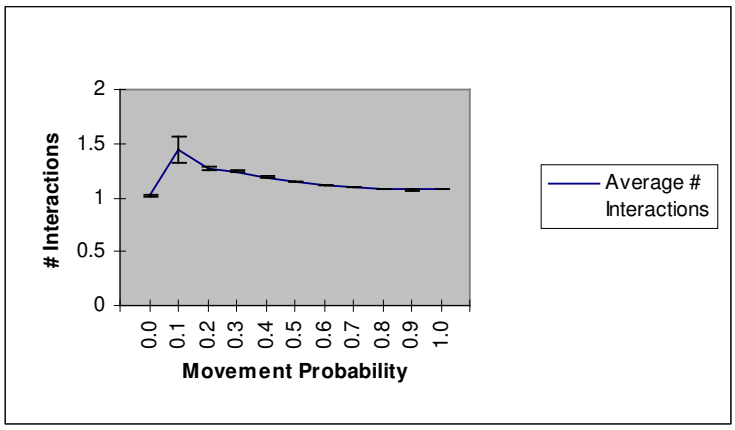

Figure 5.8. Average Number of Interactions in the EPD

Figure 5.8 shows the average number of interactions in the model. The number of interactions increases as movement probability decreases to 0.1, then abruptly drops to just above 1. The average number of interactions in the Evolutionary Prisoner's Dilemma is consistently lower than in the no-selection case presented in figure 5.3.

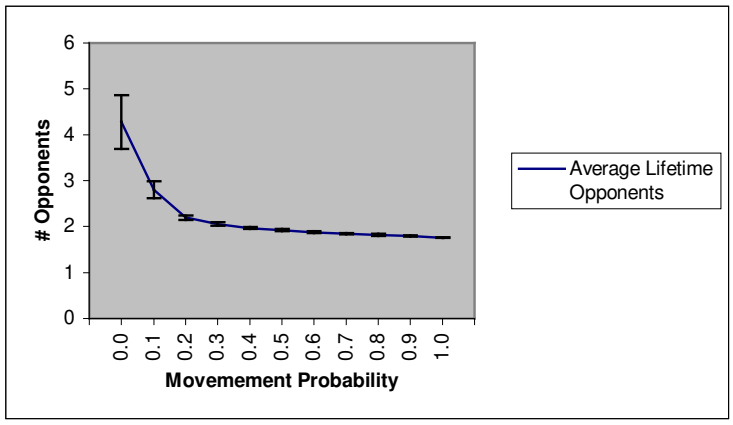

Figure 5.9. Average Lifetime Opponents in the EPD

Figure 5.9 presents the average number of lifetime opponents, which increases as movement probability decreases to 0. As with the average number of interactions, the average number of lifetime opponents in the Evolutionary Prisoner's Dilemma is consistently lower than in the no-selection case.

5.4.3 Results at Low Movement Probabilities

As can be seen from the results presented in the preceding section, there is a sudden discontinuity in the behaviour of the model between movement probabilities 0 and 0.1. This is seen in the abrupt changes in average cooperation level and average number of interactions between these two movement probabilities. Figures 5.10 to 5.12 below present results from a closer investigation of the average cooperation level, average relatedness level and average number of interactions at low movement probabilities. The average relatedness level was calculated only on the loci subject to kin selection for altruism, using relatedness

measure $\overline{r_2}$. The parameters of the model are the same as those presented in table 5.2, except the movement probability range is from 0 to 0.2, with increments of 0.02.

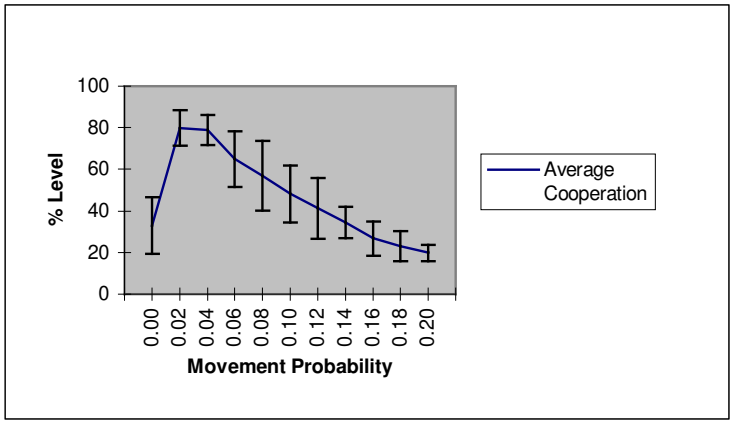

Figure 5.10. Average Cooperation in the EPD at Low Movement Probabilities

Figure 5.10 shows that in fact the average cooperation level under low movement probabilities is substantially higher than can be seen from the initial investigation of the cooperation level presented in figure 5.5, reaching around 80% at movement probability 0.02 and subsequently falling significantly at movement probability 0.

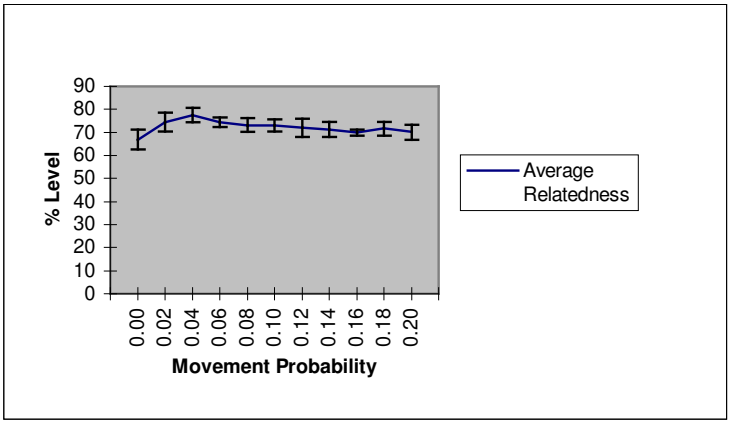

Figure 5.11. Average Relatedness at Loci Subject to Kin Selection in the EPD at Low Movement Probabilities

Figure 5.11 shows the average relatedness level $\overline{r_2}$, calculated only on the loci subject to kin selection for altruism. The relatedness level remains consistently high, showing a slight increase as movement probability decreases to 0.04, followed by a decrease as movement probability approaches 0.

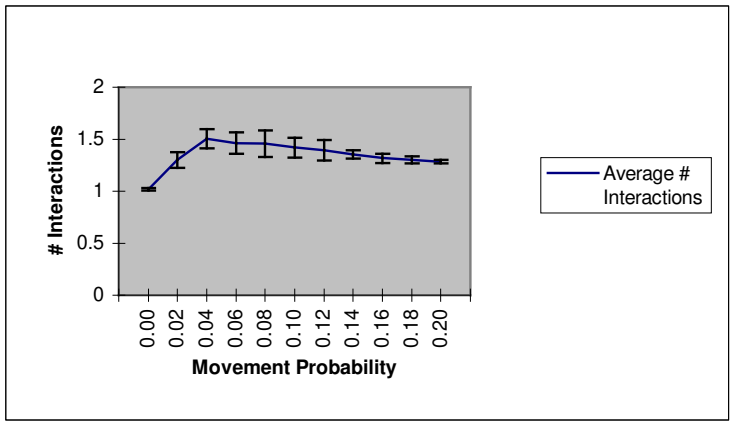

Figure 5.12. Average Number of Interactions in the EPD at Low Movement Probabilities

Figure 5.12 shows the average number of interactions, which increase as movement probability decreases to 0.04 and subsequently decrease as movement probability approaches 0. However the average number of interactions does not reach any significantly higher level than that seen in figure 5.8.

5.4.4 Results at Very Low Movement Probabilities

In the results presented in the preceding section, there is still a discontinuity in the behaviour of the model between movement probabilities 0 and 0.02, as can be seen in the abrupt change in the average cooperation level between these two movement probabilities. Figures 5.13 to 5.15 below present results for the average cooperation level, average relatedness level and average number of interactions in the Evolutionary Prisoner's Dilemma at very low movement probabilities. The average relatedness level was calculated only on the loci subject to kin selection for altruism, using relatedness measure $\overline{r_2}$. The parameters of the model are the same as those presented in table 5.2, except the movement probability range is from 0 to 0.02, with increments of 0.002.

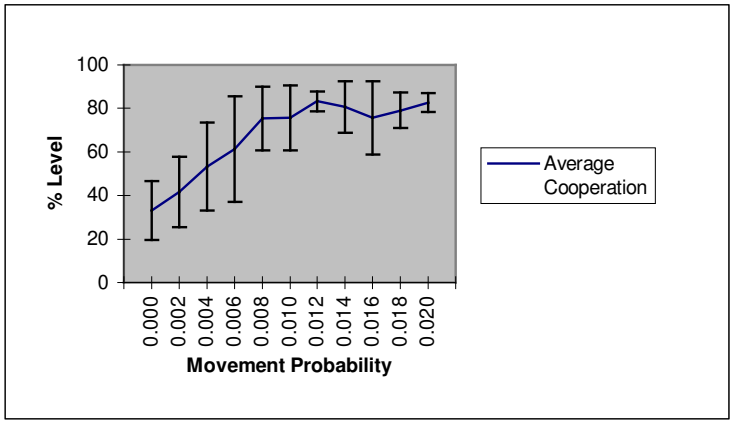

Figure 5.13. Average Cooperation in the EPD at Very Low Movement Probabilities

Figure 5.13 shows the average cooperation level decreasing continuously as it approaches movement probability 0. The discontinuity in cooperation level observed at higher movement probabilities as shown in figures 5.5 and 5.10 is not present at very low movement probabilities.

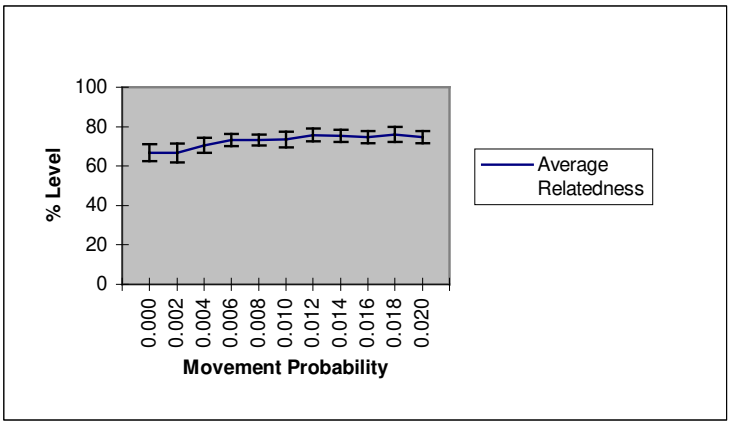

Figure 5.14. Average Relatedness on Loci Subject to Kin Selection in the EPD at Very Low Movement Probabilities

Figure 5.14 shows the average relatedness level remaining consistently high across all movement probabilities, with a slight tendency to decrease as movement probability decreases to 0.

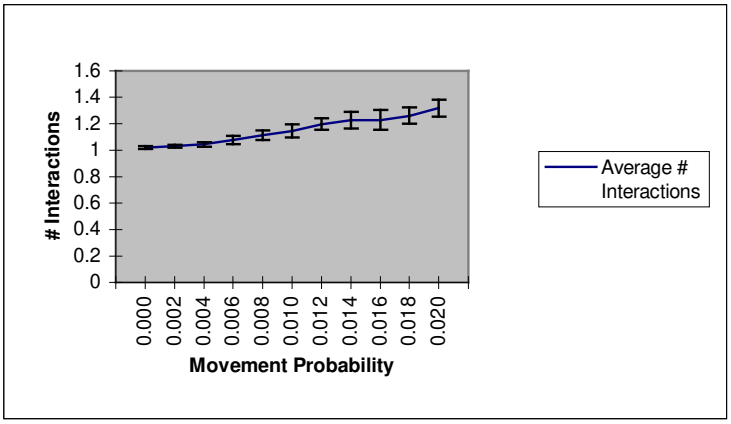

Figure 5.15. Average Number of Interactions in the EPD at Very Low Movement Probabilities

Figure 5.15 shows the average number of interactions decreasing to 1 as movement probability decreases to 0.

5.5 Results from the Pure Kin Selection Model

5.5.1 Description

This section presents results from the pure kin selection model described in chapter 4. The model parameters used to obtain these results are the same as those presented above in table 5.2.

5.5.2 Results

The results from the model are presented in figures 5.16 and 5.17 below.

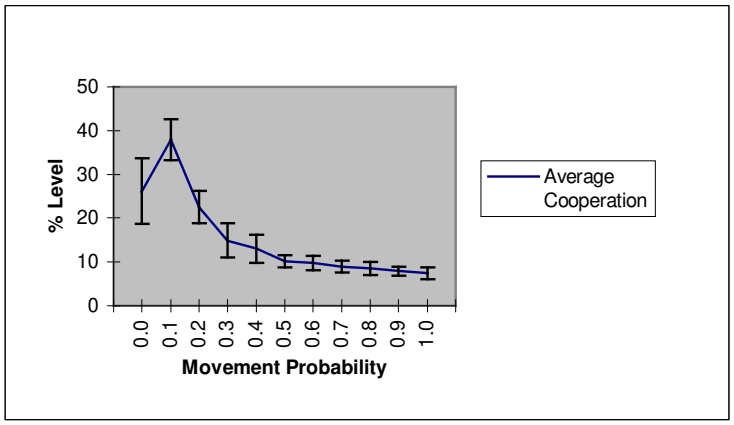

Figure 5.16. Average Cooperation in the Pure Kin Selection Model

The average cooperation curve for the pure kin selection model, presented in figure 5.16, demonstrates a striking similarity to the average cooperation curve for the Evolutionary Prisoner's Dilemma presented in figure 5.5. Both curves exhibit an increase in cooperation level as movement probability approaches 1, followed by a drop in cooperation level at movement probability 0. The main difference between figure 5.16 and figure 5.5 is the magnitude of the average cooperation level, which is lower in figure 5.16.

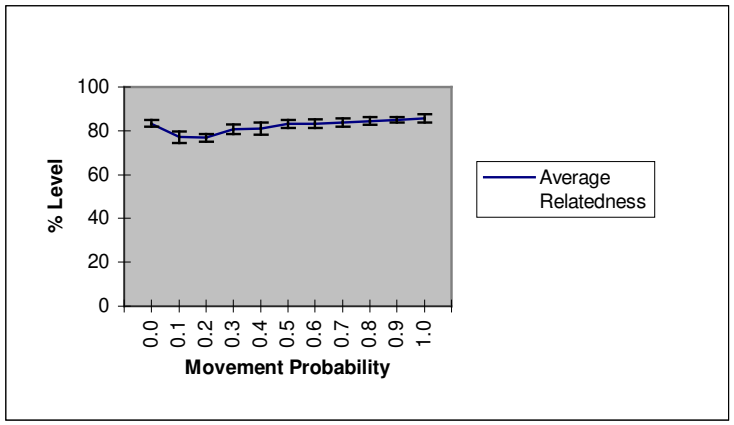

Figure 5.17. Average Relatedness in the Pure Kin Selection Model

Figure 5.17 shows the average relatedness level, which shows a slight decrease in relatedness level as movement probability decreases to 0.2, followed by a slight increase as movement probability decreases to 0. This behaviour is the opposite of that observed in the Evolutionary Prisoner's Dilemma model both with and without selection and presented in figures 5.6 and 5.2 respectively. In these models, the relatedness level increases as movement probability decreases to 0.1, then decreases as movement probability reaches 0.

5.5.3 Results at Low Movement Probabilities

The results presented in the preceding section show a discontinuity in the average cooperation level between movement probabilities 0 and 0.1. Figures 5.18 and 5.19 present results for the average cooperation level and average relatedness in the pure kin selection model at low movement probabilities.

The parameters of the model are the same as those presented in table 5.2, except the movement probability range is from 0 to 0.2, with increments of 0.02.

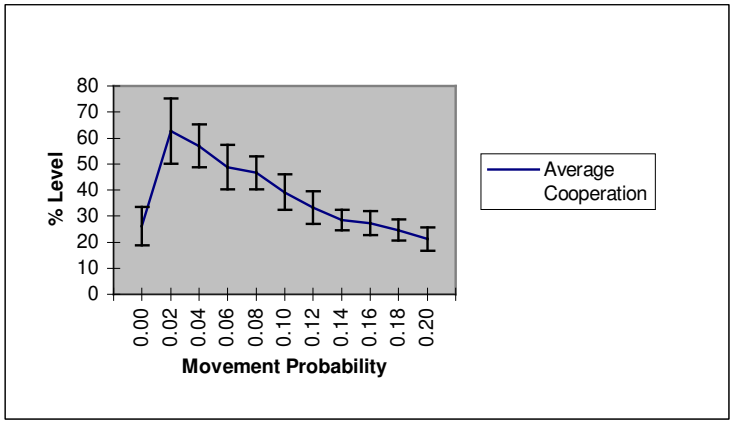

Figure 5.18. Average Cooperation in the Pure Kin Selection Model at Low Movement Probabilities

Figure 5.18 shows the average cooperation level increasing as movement probability decreases to 0.02, followed by a substantial drop in cooperation level at movement probability 0. This behaviour echoes that of the Evolutionary Prisoner's Dilemma at low movement probabilities, as shown in figure 5.10, but again the magnitude of the cooperation level is reduced in the pure kin selection model.

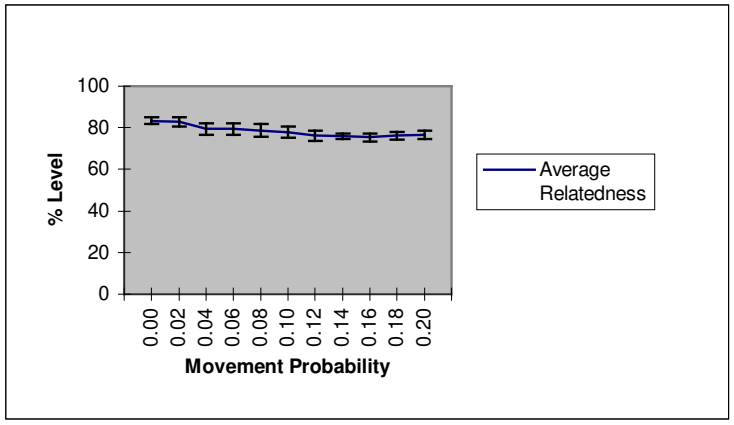

Figure 5.19. Average Relatedness in the Pure Kin Selection Model at Low Movement Probabilities

Figure 5.19 shows the average relatedness level remaining high across all movement probabilities, and increasing slightly as movement probability decreases to 0.

5.5.4 Results at Very Low Movement Probabilities

In the results presented in the preceding section, there is still a discontinuity in the average cooperation level in the model between movement probabilities 0 and 0.02. Figures 5.20 and 5.21 below present results from an examination of the average cooperation level and average relatedness at very low movement probabilities. The parameters of the model are the same as those presented in table 5.2, except the movement probability range is from 0 to 0.02, with increments of 0.002.

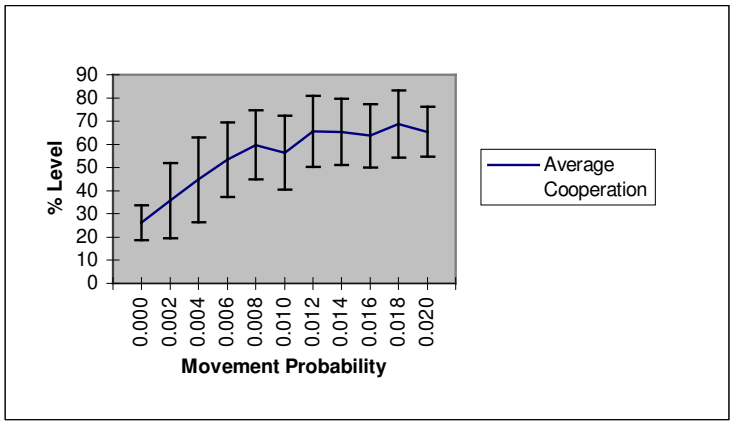

Figure 5.20. Average Cooperation in the Pure Kin Selection Model at Very Low Movement Probabilities

Figure 5.20 shows the average cooperation level decreasing continuously as movement probability approaches 0. The discontinuity observed at higher movement probabilities and shown in figures 5.16 and 26 is not present here. Once again this behaviour echoes the behaviour of the Evolutionary Prisoner's Dilemma presented in figure 5.13.

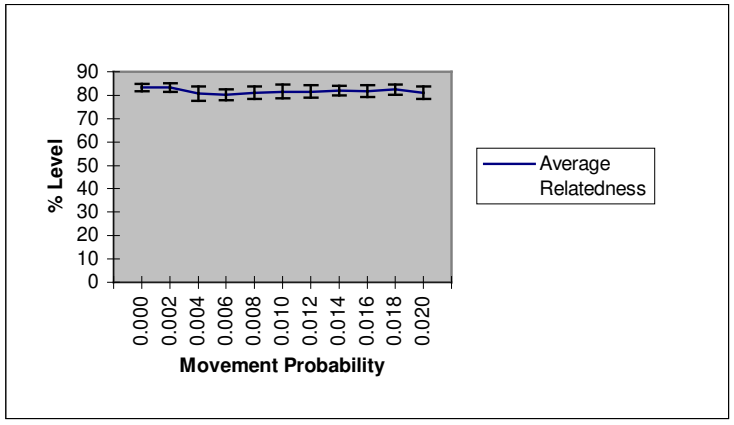

Figure 5.21. Average Relatedness in the Pure Kin Selection Model at Very Low Movement Probabilities

Figure 5.21 shows the average relatedness level remaining consistently high across all movement probabilities, with little discernible variation.

5.5.5 Results with Long Agent Lifespan

In order to determine if increasing the average agent lifespan changes the behaviour of the pure kin selection model, this section presents results in which the model configuration is as described in table 5.2, except that the initial agent energy is increased to 30. The results are presented in figures 5.22 and 5.23 below.

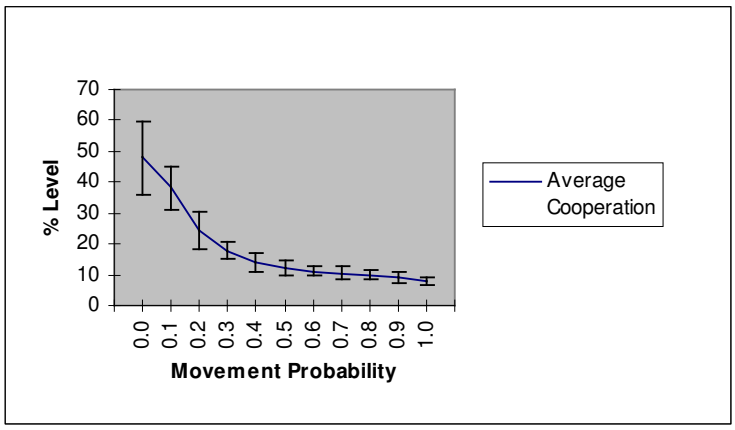

Figure 5.22. Average Cooperation in the Pure Kin Selection Model with Long Agent Lifespan

Figure 5.22 shows the average cooperation level increasing continuously as movement probability decreases, reaching the mean cooperation level at movement probability 0 where it is noisy around this point. By comparing the cooperation level shown in figure 5.22 with that for the pure kin selection model with shorter agent lifespan shown in figure 5.16, it can be seen that the effect of increasing agent lifespan has been to eliminate the discontinuity in cooperation level between movement probabilities 0 and 0.1.

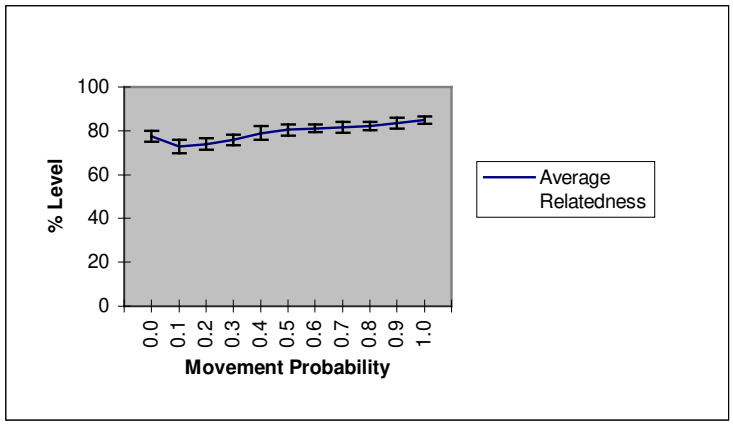

Figure 5.23. Average Relatedness in the Pure Kin Selection Model with Long Agent Lifespan

The average relatedness level presented in figure 5.23 is very similar to that for the pure kin selection model with shorter agent lifespan shown in figure 5.17.

5.6 Results from the Pure Reciprocal Cooperation Model

5.6.1 Description

This section presents results from the pure reciprocal cooperation model described in chapter 4. The model parameters for these results are those presented above in table 5.2.

5.6.2 Results

The results from the model are presented in figures 5.24 to 5.27 below.

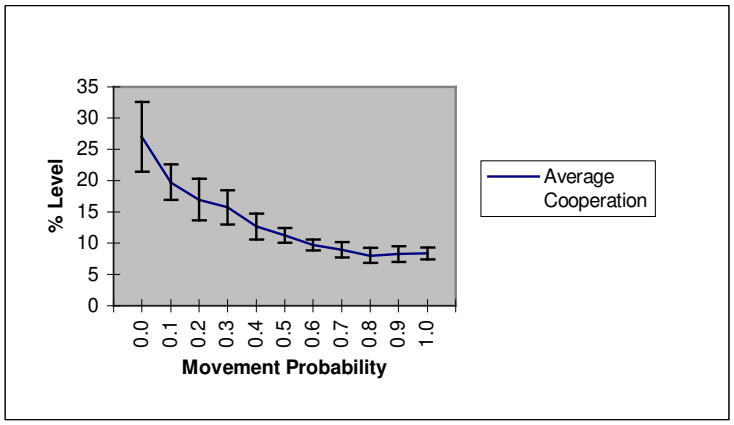

Figure 5.24. Average Cooperation in the Pure Reciprocal Cooperation Model

Figure 5.24 shows the average cooperation level increasing continuously as movement probability decreases to 0. The maximum cooperation level achieved is low, at slightly above 25%.

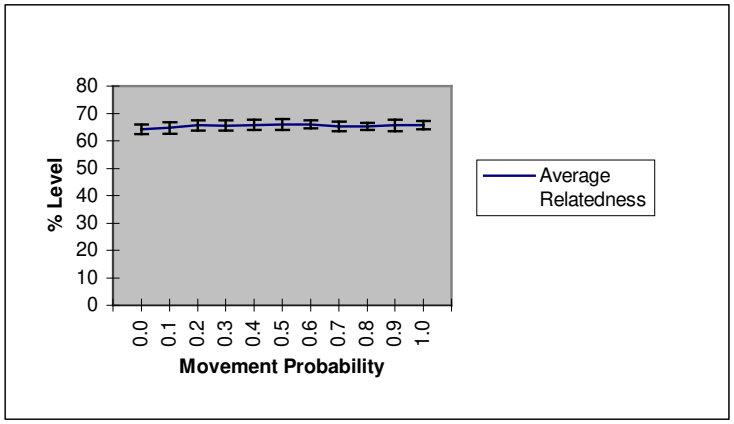

Figure 5.25. Average Relatedness in the Pure Reciprocal Cooperation Model

Figure 5.25 shows the average relatedness level remaining consistently high, above 60%, across all movement probabilities, with no discernible variation.

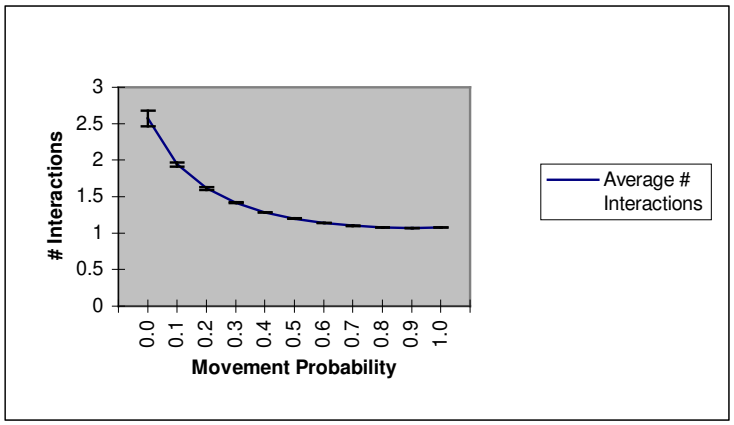

Figure 5.26. Average Number of Interactions in the Pure Reciprocal Cooperation Model

Figure 5.26 shows the average number of interactions increasing continuously from slightly above 1 to slightly above 2.5 as movement probability decreases to 0.

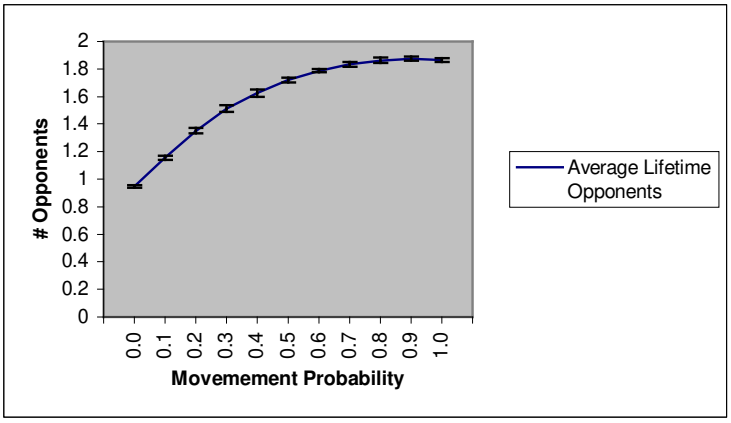

Figure 5.27. Average Lifetime Opponents in the Pure Reciprocal Cooperation Model

Figure 5.27 shows the average number of lifetime opponents, which decreases to 1 as movement probability decreases to 0.

5.6.3 Results with Long Agent Lifespan

In order to determine if increasing the average agent lifespan changes the behaviour of the pure reciprocal cooperation model, this section presents results in which the model configuration is as described in table 5.2, except that the initial agent energy is increased to 30. The results are presented in figures 5.28 to 5.31 below.

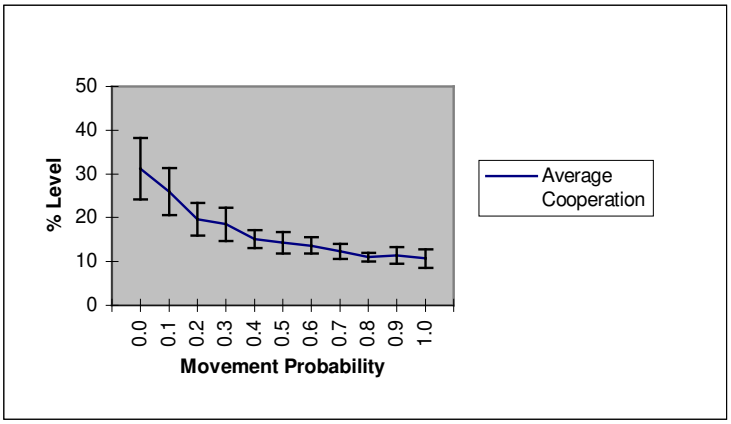

Figure 5.28. Average Cooperation in the Pure Reciprocal Cooperation Model with Long Agent Lifespan

Figure 5.28 shows the average cooperation level behaving similarly to the cooperation level for the pure reciprocal cooperation model with shorter agent lifespan, presented in figure 5.24. The apparent effect of increasing agent lifespan is a slight increase in the cooperation level across all movement probabilities.

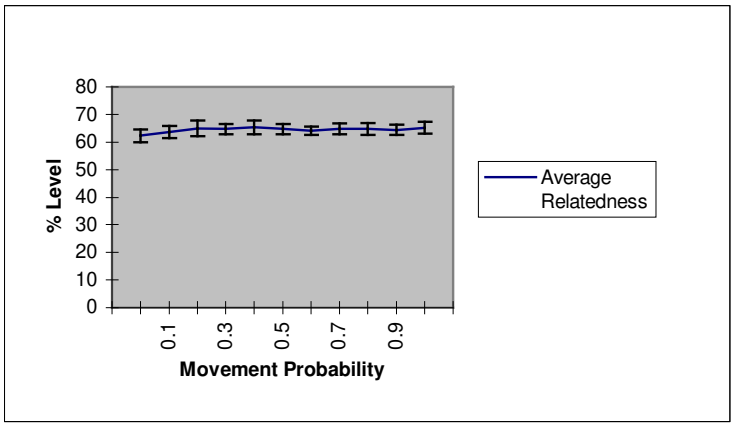

Figure 5.29. Average Relatedness in the Pure Reciprocal Cooperation Model with Long Agent Lifespan

Figure 5.29 shows an average relatedness level that is consistently high, around 60%, across all movement probabilities, and which does not vary noticeably with movement probability.

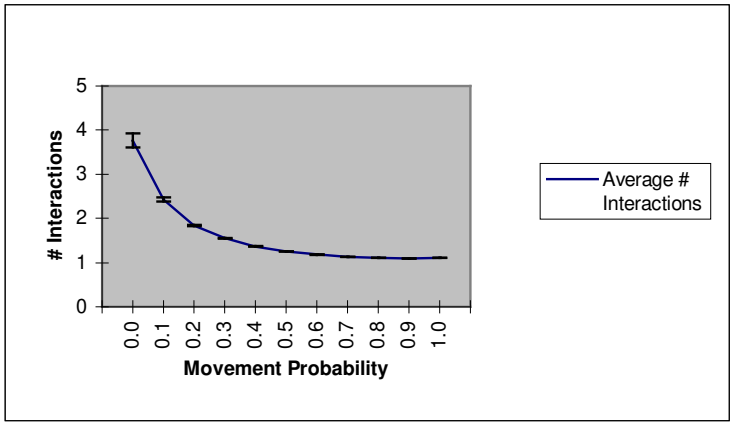

Figure 5.30. Average Number of Interactions in the Pure Reciprocal Cooperation Model with Long Agent Lifespan

Comparing figure 5.30 with figure 5.26 shows that lengthening the agent lifespan has significantly increased the average number of interactions at the lower movement probabilities in the pure reciprocal cooperation model.

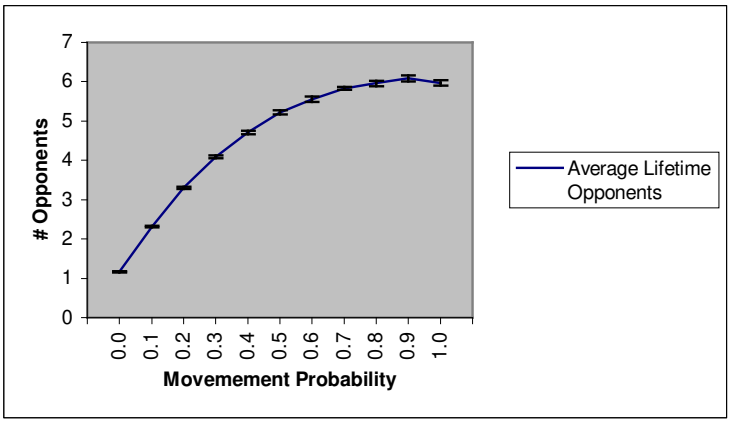

Figure 5.31. Average Lifetime Opponents in the Pure Reciprocal Cooperation Model with Long Agent Lifespan

Similarly, comparing figure 5.31 with figure 5.27 shows that lengthening the agent lifespan has significantly increased the average number of lifetime opponents in the pure reciprocal cooperation model, in this case by a factor of 3 at movement probability 1. However the average number of lifetime opponents still approaches 1 as movement probability approaches 0.

5.7 Results of Local Population Regulation

5.7.1 Description

This section presents results obtained by applying local population regulation to the Evolutionary Prisoner's Dilemma and the pure kin selection model. The motivation for this was given in section 3.3. The parameters of both these models are as given in table 5.2. The models are in all respects identical to their original forms, except that the population is regulated at a cell level rather than at a global level, with a maximum cell population of 5.

5.7.2 Results from the Evolutionary Prisoner's Dilemma with Local Population Regulation

The results from the Evolutionary Prisoner's Dilemma with local population regulation are presented in figures 5.32 to 5.36 below. Section 3.3 identified the interest in studying the effects of local population regulation on kin selection. In this experiment local population regulation was implemented by preventing reproduction in any cell in which the population size has reached 5.

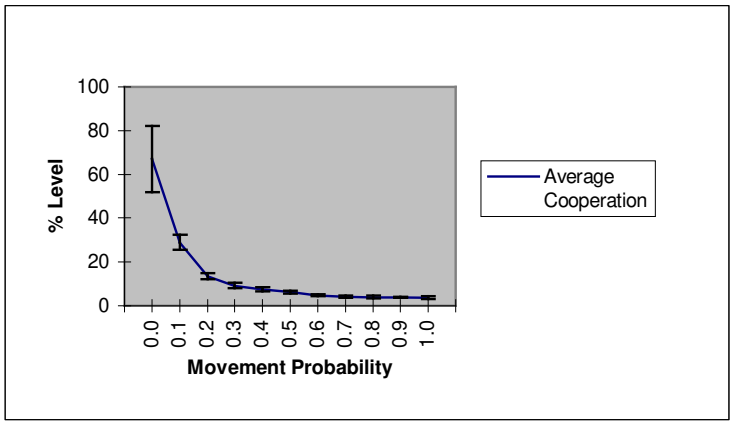

Figure 5.32. Average Cooperation in the EPD with Local Population Regulation

Figure 5.32 shows the average cooperation level continuously increasing as movement probability decreases to 0. Comparing the cooperation level presented in figure 5.32 with that for the Evolutionary Prisoner's Dilemma presented in figure 5.5, the change from global population regulation to local population regulation appears to have both decreased the average cooperation level across all movement probabilities except movement probability 0, and removed the discontinuity in cooperation level between movement probabilities 0 and 0.1.

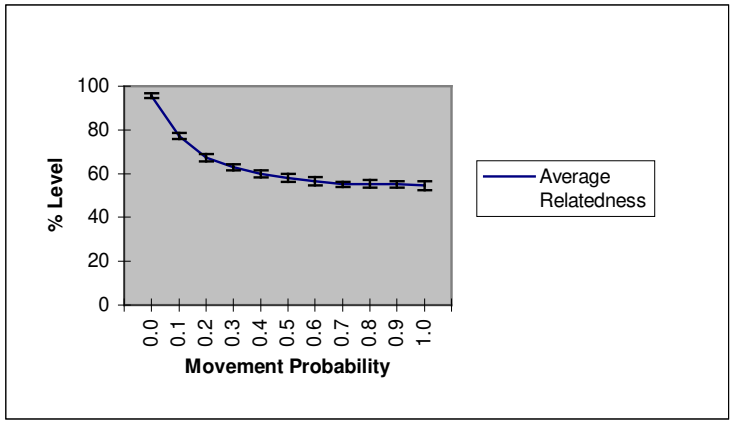

Figure 5.33. Average Relatedness on Loci Subject to Kin Selection in the EPD with Local Population Regulation

Figure 5.33 shows the average relatedness level $\overline{r_2}$ increasing continuously to a level just below 100% as movement probability decreases to 0.

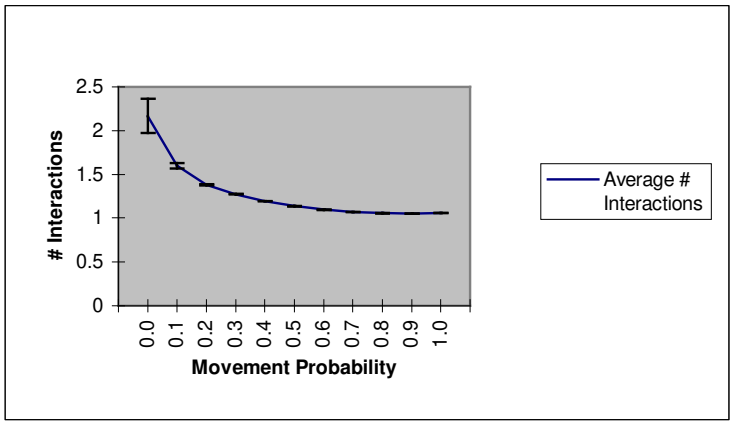

Figure 5.34. Average Number of Interactions in the EPD with Local Population Regulation

Figure 5.34 shows the average number of interactions increasing continuously as movement probability decreases to 0.

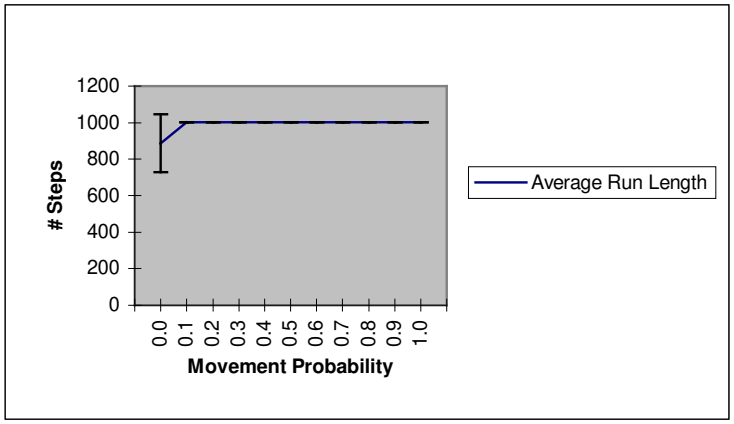

Figure 5.35. Average Run Length in the EPD with Local Population Regulation

Figure 5.35 shows that not all simulations ran to completion at movement probability 0, but some were terminated prematurely due to the agent population becoming extinct.

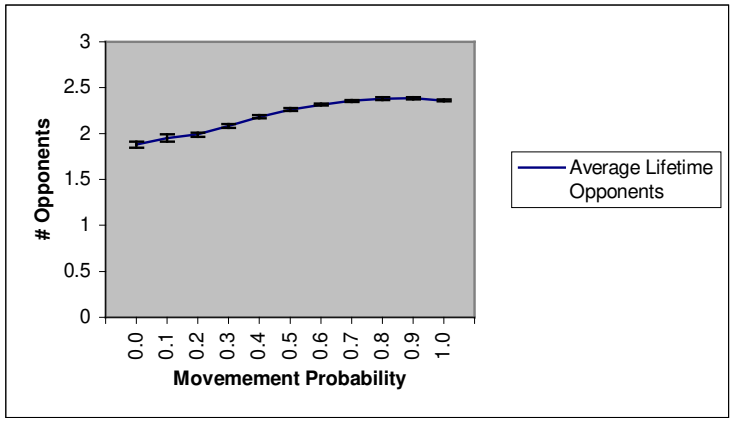

Figure 5.36. Average Lifetime Opponents in the EPD with Local Population Regulation

Figure 5.36 shows the average number of lifetime opponents decreasing continuously to less than 2 as movement probability decreases to 0.

5.7.3 Results from the Pure Kin Selection Model with Local Population Regulation

Figures 5.37 to 5.39 below present the results from the pure kin selection model with local population regulation. Local population regulation was implemented Section 3.3 identified the interest in studying the effects of local population regulation on kin selection. In this experiment local population regulation was implemented by preventing reproduction in any cell in which the population size has reached 5. Section 3.3 gave the motivation for studying the effects of local population regulation on kin selection.

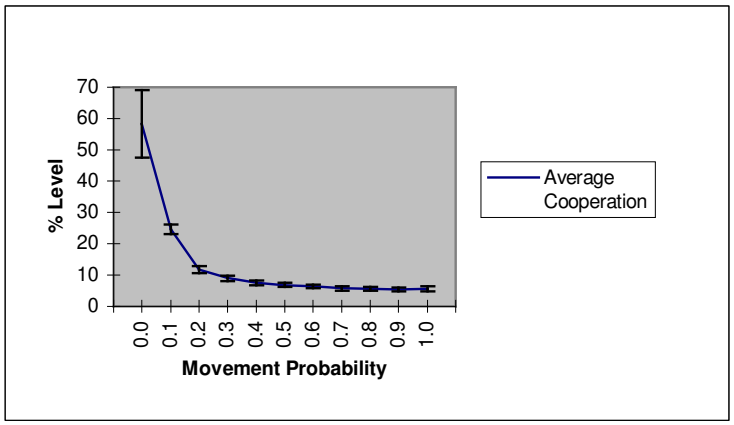

Figure 5.37. Average Cooperation in the Pure Kin Selection Model with Local Population Regulation

Figure 5.37 shows the average cooperation level rising slightly between movement probabilities 1 and 0.2, yet remaining at around 10%. As movement probability decreases from 0.2 to 0 there is a sharp increase in cooperation to above 50%.

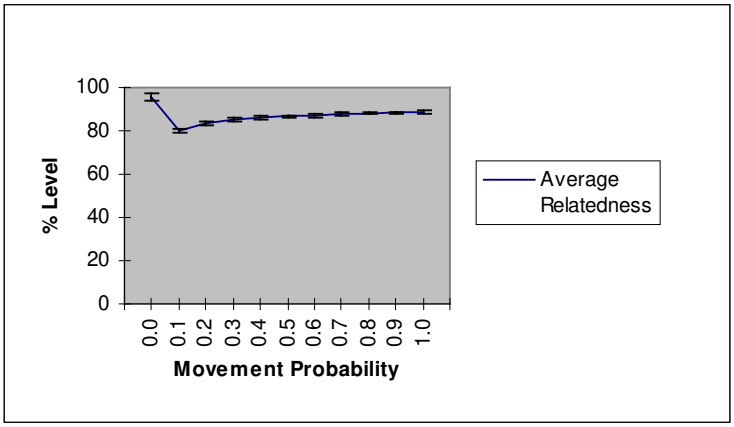

Figure 5.38. Average Relatedness in the Pure Kin Selection Model with Local Population Regulation

Figure 5.38 shows average relatedness decreasing slightly as movement probability decreases from 1 to 0.1, then increasing at movement probability 0. The average relatedness level is high at all movement

probabilities, staying consistently above 80%. This behaviour is similar to that in the standard pure kin selection model, presented in figure 5.17.

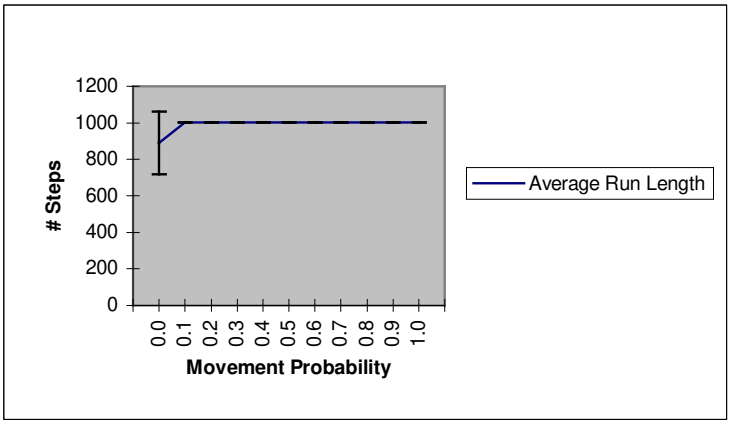

Figure 5.39. Average Run Length in the Pure Kin Selection Model with Local Population Regulation

Figure 5.39 shows that, as in the Evolutionary Prisoner's Dilemma with local population regulation, not all simulations ran to completion at movement probability 0, but some were terminated prematurely due to the agent population becoming extinct.

5.8 Results from the Evolutionary Prisoner's Dilemma with Modifications from Oliphant's Model

This section presents results from experiments based on the Evolutionary Prisoner's Dilemma with modifications motivated by Oliphant's (1994) model. The modifications made to the Evolutionary Prisoner's Dilemma are to change the Prisoner's Dilemma payoffs used to Oliphant's defector-disadvantageous payoffs, which as noted in chapter 2 do not strictly satisfy the requirements for a Prisoner's Dilemma, and to study a one-dimensional environment.

5.8.1 Defector-Disadvantageous Payoffs

Oliphant (1994) used a payoff matrix that reduced the advantage to defectors to increase the stability of cooperation in his model. This section presents results from the Evolutionary Prisoner's Dilemma using Oliphant's payoffs, which are presented in table 5.2 below.

	C	**D**
C	4.5, 4.5	0, 5
D	5, 0	0.5, 0.5

Table 5.2. Oliphant's Prisoner's Dilemma Payoff Matrix

(note: payoffs to the row player are listed first)

As noted in section 2.4.1, Oliphant's payoff matrix does not actually satisfy the requirement $\boldsymbol{R} > (\boldsymbol{T} + \boldsymbol{S}) / 2$ for a Prisoner's Dilemma.

As the Evolutionary Prisoner's Dilemma only allows payoffs to be specified as integers, Oliphant's payoffs are multiplied by 10 to give $\boldsymbol{T} = 50$, $\boldsymbol{R} = 45$, $\boldsymbol{P} = 5$ and $\boldsymbol{S} = 0$. Similarly the initial agent energy

and energy living cost are multiplied by 10, to be 150 and 30 respectively. The remaining model parameters are the same as those presented in table 5.2.

The results from the model are presented in figures 5.40 to 5.43 below.

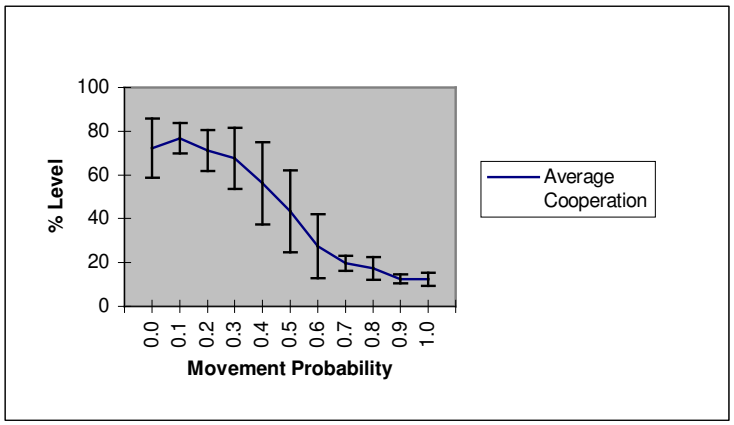

Figure 5.40. Average Cooperation in the EPD with Oliphant's Payoffs

Figure 5.40 shows the average cooperation level increasing continuously to a high level as movement probability decreases to 0. However the cooperation level shown is somewhat noisy.

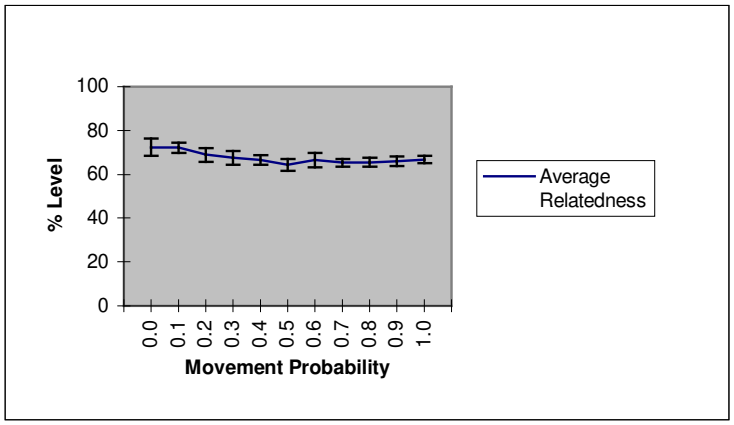

Figure 5.41. Average Relatedness in the EPD with Oliphant's Payoffs

Figure 5.41 shows that the average relatedness level is consistently high, around 70% across all movement probabilities, and has a slight tendency to increase as movement probability decreases to 0.

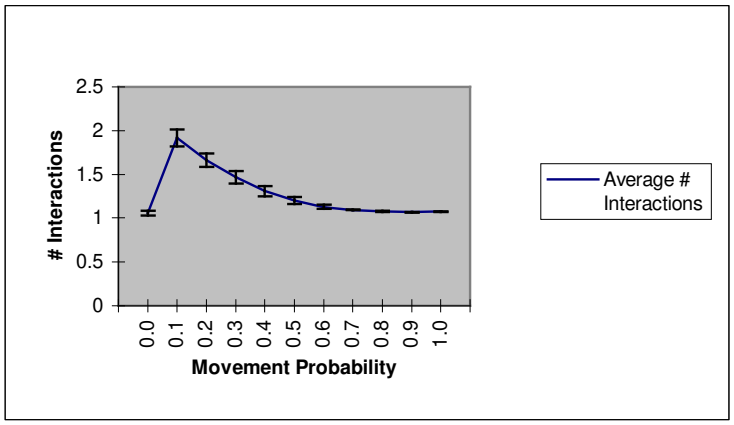

Figure 5.42. Average Number of Interactions in the EPD with Oliphant's Payoffs

Figure 5.42 shows the average number of interactions increasing from just above 1 to just below 2 as movement probability decreases to 0.1, then dropping back to just above 1 again at movement probability 0.

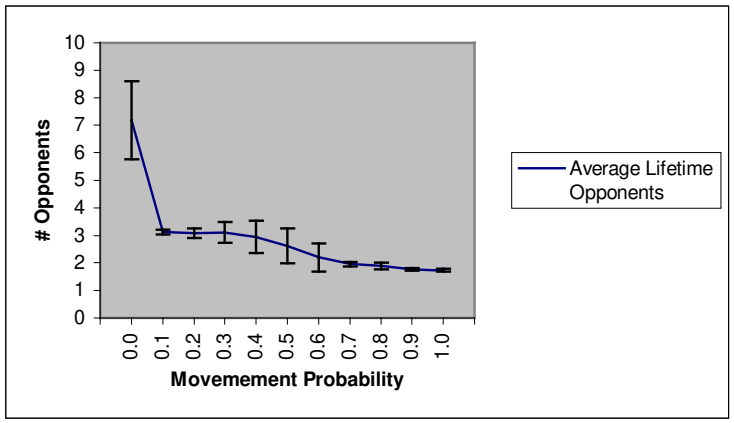

Figure 5.43. Average Lifetime Opponents in the EPD with Oliphant's Payoffs

Figure 5.43 shows the average number of lifetime opponents increasing as movement probability decreases to 0, with a large increase between movement probabilities 0.1 and 0.

5.8.2 One-Dimensional Environment

This section presents results from the Evolutionary Prisoner's Dilemma using a one-dimensional environment as in Oliphant's (1994) model. The Prisoner's Dilemma payoffs used in this experiment are those presented in table 1.1. The model parameters are the same as those presented in table 5.2, except that the vertical world size is changed to 1.

The results from the model are presented in figures 5.44 to 5.47 below.

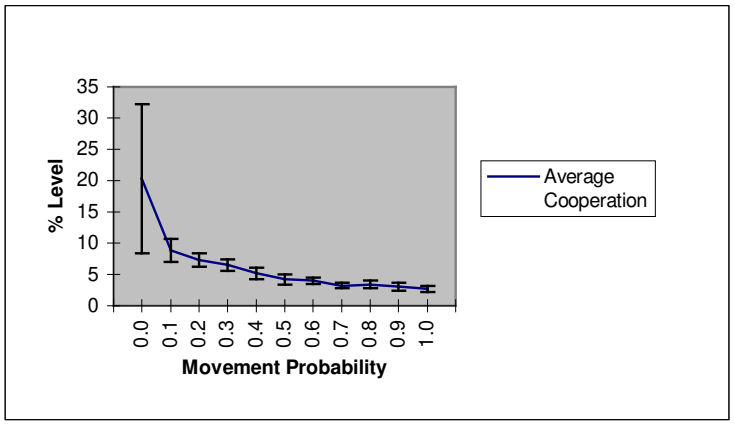

Figure 5.44. Average Cooperation in the One-Dimensional EPD

Figure 5.44 shows the average cooperation level continuously increasing as movement probability decreases to 0, with a noisy cooperation level at movement probability 0. The average cooperation level across all movement probabilities is low, only approaching 20% at movement probability 0.

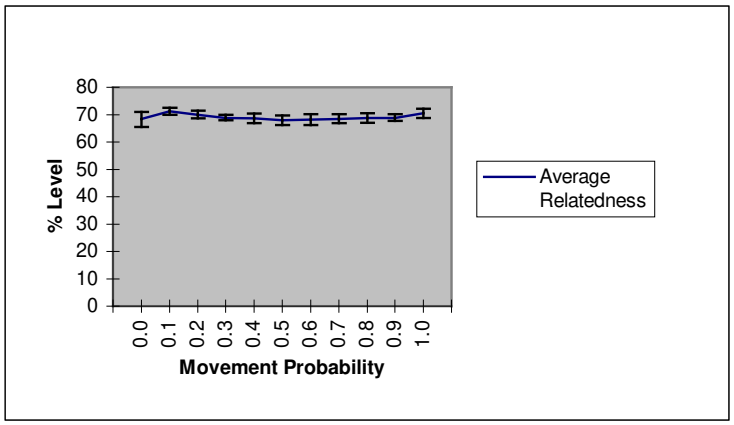

Figure 5.45. Average Relatedness in the One-Dimensional EPD

Figure 5.45 shows the average relatedness level remaining consistently high, around 70% across all movement probabilities, with no clear variation.

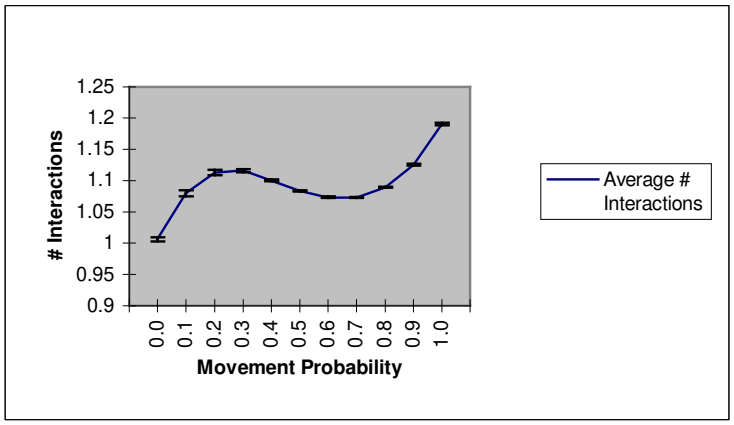

Figure 5.46. Average Number of Interactions in the One-Dimensional EPD

Figure 5.46 shows an interesting curve for the average number of interactions, which the scale of the graph has been chosen to emphasise. The curve exhibits a local peak of number of interactions at movement probability 0.3, and a local minimum of number of interactions at movement probability 0.7. Both the peak and the minimum are within the average number of interactions at either end of the movement probability scale. Additionally, the curve exhibits a high degree of rotational symmetry, so that if it is rotated through 180 degrees it is still a good fit to itself.

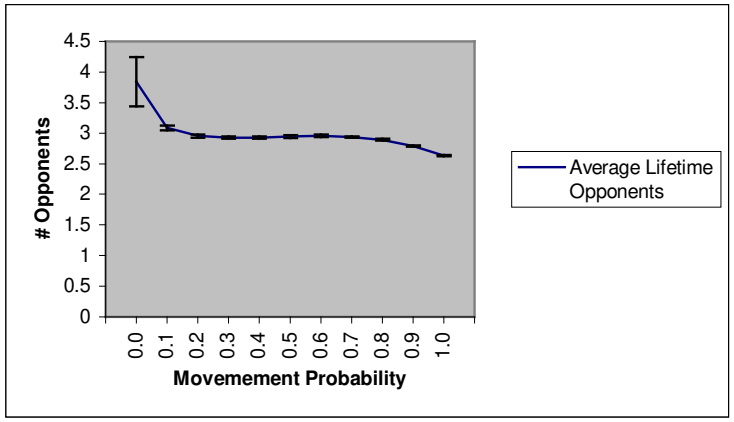

Figure 5.47. Average Lifetime Opponents in the One-Dimensional EPD

Figure 5.47 shows the average number of lifetime opponents increasing to nearly 4 as movement probability decreases to 0.

5.9 Results from the Extended Interaction Length Evolutionary Prisoner's Dilemma

5.9.1 Description

This section presents results from a variant of the Evolutionary Prisoner's Dilemma, which plays three rounds of the Prisoner's Dilemma instead of one at each interaction between two agents.

This modification to the Evolutionary Prisoner's Dilemma is motivated by the observation that average interaction lengths are low, typically below two, and by the desire to study longer interaction histories that reach or exceed the number of interactions required for the collective stability of Tit-for-Tat, which is used as an indicator of the support for reciprocal cooperation as described in section 6.3.1. The parameters of the model are the same as those presented in table 5.2, except that initial agent energy is increased to 45 and living cost is increased to 9, to reflect the increased payoffs agents can receive over each timestep due to increased interaction length.

5.9.2 Results

The results from the model are presented in figures 5.48 and 5.49 below.

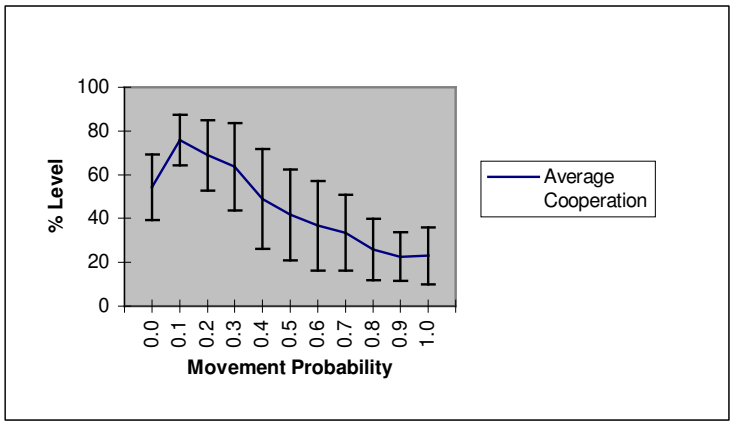

Figure 5.48. Average Cooperation in the EPD with Extended Interaction Length

Figure 5.48 shows a noisy average cooperation level that increases as the movement probability approaches 0.1. The average cooperation level is substantially higher than that in the standard Evolutionary Prisoner's Dilemma presented in section 5.4.2.

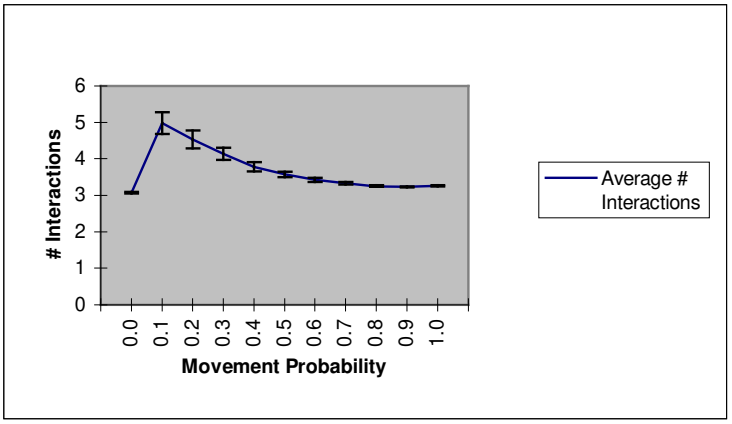

Figure 5.49. Average Number of Interactions in the EPD with Extended Interaction Length

Figure 5.49 shows an average number of interactions that is substantially higher than that in the standard Evolutionary Prisoner's Dilemma presented in section 5.4.2. The average number of interactions

increases as movement probability decreases to 0.1, then falls to its lowest possible level at movement probability 0.

5.10 Results from the Evolutionary Prisoner's Dilemma Using Battle of the Sexes Payoffs

5.10.1 Description

This section presents results from using the payoffs from the Battle of the Sexes game, described in section 1.3.4, in the Evolutionary Prisoner's Dilemma. The model parameters are those presented in table 5.2. The payoff matrix was chosen such that an interacting pair of agents need to swap roles during the course of their interaction in order to share the payoffs fairly and so ensure their mutual survival. Therefore, given a living cost of 3 energy units per timestep, payoffs were chosen that give an average payoff of 3 energy units per timestep if interacting agents swap roles over time. The payoff matrix used is presented in table 5.3 below.

	A	**B**
A	1,1	2,4
B	4,2	0,0

Table 5.3. Battle of the Sexes Payoff Matrix

(note: payoffs to the role player are listed first)

Rather than measuring cooperation as the percentage of cooperative actions performed as described in section 5.2.1, cooperation for this model was measured as the percentage of times agents coordinated on either of the outcomes AB or BA. Let $\boldsymbol{J_{ab}}$ be the set of interactions performed by a pair of agents $\{a,b\} \in \bar{I}$. Then let $\boldsymbol{K_{ab}}$ be the set of these interactions which are either AB or BA, so $K_{ab} \subset J_{ab}$ and $(A \in \{a',b'\} \wedge B \in \{a',b'\}) \forall \{a',b'\} \in K_{ab}$. Then the average cooperation level is

$$\overline{c_2} = 100 \frac{\sum \left(|K_{ab}| \div |J_{ab}| \right)}{|\bar{I}|} \forall \{a,b\} \in \bar{I}$$

5.10.2 Results

The results from the model are presented in figures 5.50 to 5.52 below.

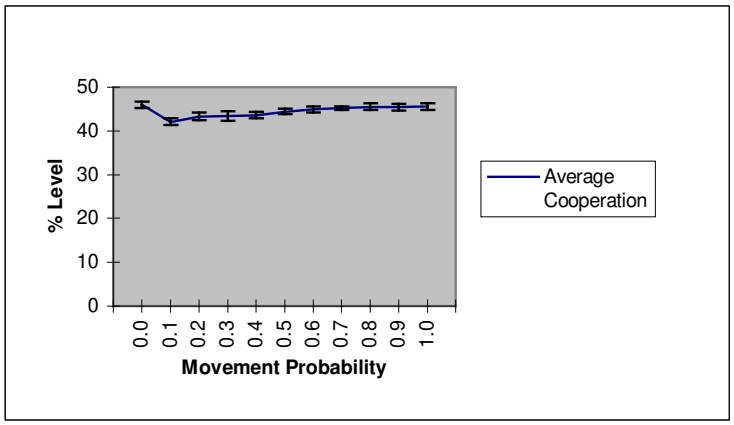

Figure 5.50. Average Cooperation in the EPD with Battle of the Sexes Payoffs

Figure 5.50 shows the average cooperation level decreasing slightly from movement probability 0 to movement probability 0.1, followed by a slight rise at movement probability 0. Across all movement probabilities the cooperation level is slightly below the mean.

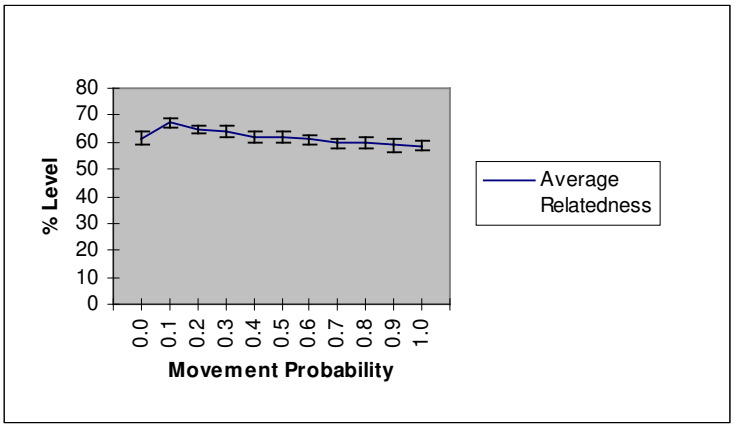

Figure 5.51. Average Relatedness in the EPD with Battle of the Sexes Payoffs

Figure 5.51 shows the average relatedness remaining consistently high across all movement probabilities, and showing a slight increase as movement probability decreases to 0.1, followed by a slight decrease again at movement probability 0.

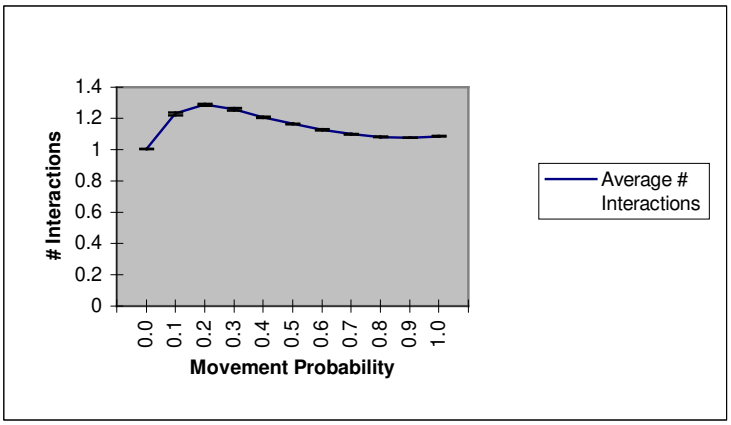

Figure 5.52. Average Number of Interactions in the EPD with Battle of the Sexes Payoffs

Figure 5.52 shows the average number of interactions increasing from movement probability 1 to movement probability 0.2, followed by a decrease as movement probability decreases to 0. At all movement probabilities the average number of interactions is very low, reaching approximately 1.3 at its highest.

5.11 Model Visualisation

This section presents visualisations of the some of the models for which results have been presented in the preceding sections, using the visualisation technique described in section 4.6.2. Visualisations of the population at high movement probability (1), medium movement probability (0.5), low movement probability (0.1) and very low movement probability (0.01) are presented for each model. The models for which visualisations are presented are the Evolutionary Prisoner's Dilemma, the pure kin selection model and the pure reciprocal cooperation model. For all the models the relatedness level in a cell on any timestep was calculated as the average of the relatedness of all pairs of agents interacting in that cell on that timestep. For the Evolutionary Prisoner's Dilemma relatedness was calculated using relatedness measure $\overline{r_2}$ considering only the loci subject to kin selection for altruism identified in section 3.3.2. For the pure kin selection and pure reciprocal cooperation models relatedness was calculated over the agents' entire genotypes, using relatedness measure $\overline{r_1}$. For interpretation of the colours used in the visualisations refer back to section 4.6.2 and particularly table 4.1.

5.11.1 Visualisation of the Evolutionary Prisoner's Dilemma

Figures 5.53 to 5.56 below present visualisations of the Evolutionary Prisoner's Dilemma at movement probabilities 1, 0.5, 0.1 and 0.01 respectively.

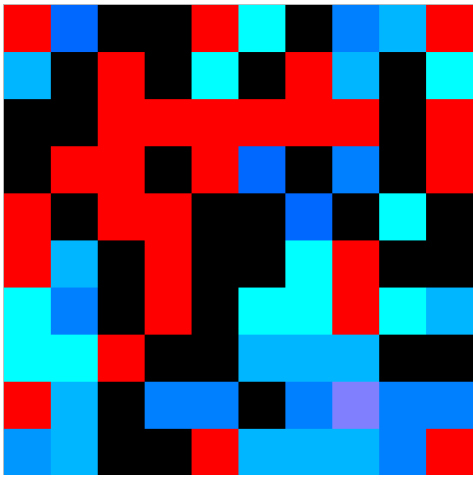

Figure 5.53. Visualisation of the EPD at Movement Probability 1

Figure 5.53 shows a widely distributed population, with many cells inhabited by single agents (red), and many cells containing populations that are either uncooperative and unrelated (blue) or uncooperative and related (cyan).

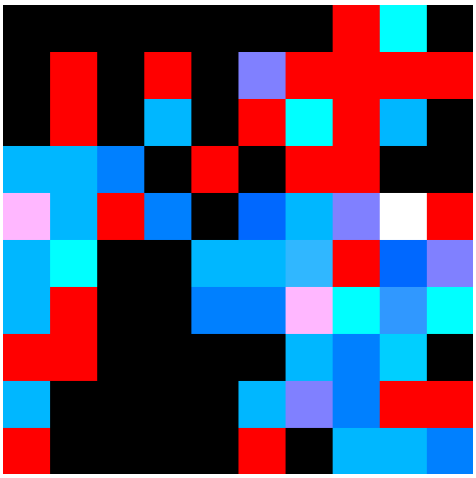

Figure 5.54. Visualisation of the EPD at Movement Probability 0.5

Figure 5.54 shows a less distributed population, once again with many cells inhabited by single agents (red) and many uncooperative unrelated (blue) or uncooperative related (cyan) cells, but also some cooperative unrelated (magenta) and cooperative related (white) cells have begun to appear.

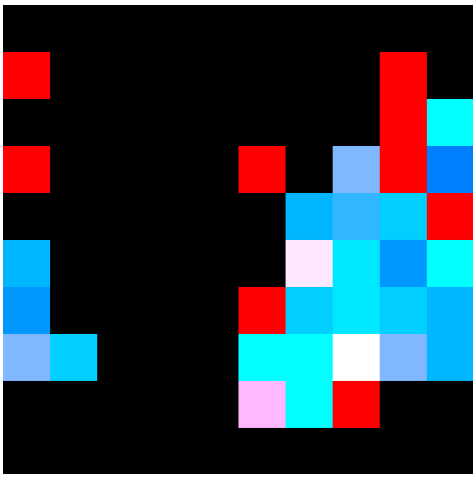

Figure 5.55. Visualisation of the EPD at Movement Probability 0.1

Figure 5.55 shows a more clustered population. Single agent cells (red) are less frequent, and uncooperative related cells (cyan) are becoming more frequent than uncooperative unrelated cells (blue). Cooperative unrelated (magenta) and cooperative related (white) cells are also present.

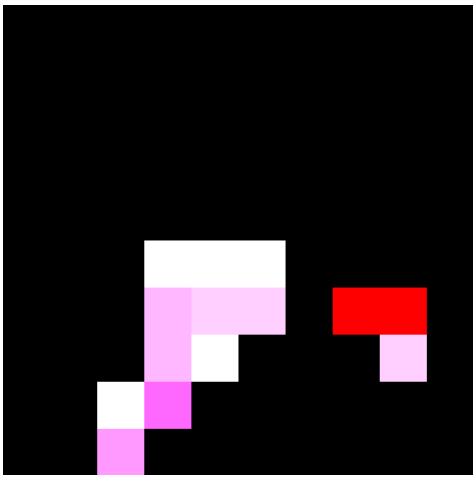

Figure 5.56. Visualisation of the EPD at Movement Probability 0.01

Figure 5.56 shows a tightly clustered population, in which cooperative unrelated (magenta) and cooperative related (white) cells dominate. Additionally, most of the cooperative unrelated cells are tending towards a higher level of relatedness, as indicated by the lighter shades of magenta.

5.11.2 Visualisation of the Pure Kin Selection Model

Figures 5.57 to 5.60 below present visualisations of the pure kin selection model at movement probabilities 1, 0.5, 0.1 and 0.01 respectively.

Figure 5.57. Visualisation of the Pure Kin Selection Model at Movement Probability 1

Figure 5.57 shows a widely distributed population dominated by cells inhabited by single agents (red) and uncooperative related cells (cyan). There are occasional uncooperative unrelated cells (blue).

Figure 5.58. Visualisation of the Pure Kin Selection Model at Movement Probability 0.5

Figure 5.58 shows a less distributed population that is still predominantly comprised of single agent cells (red) and uncooperative related cells (cyan). However the number of uncooperative unrelated cells (blue) has increased.

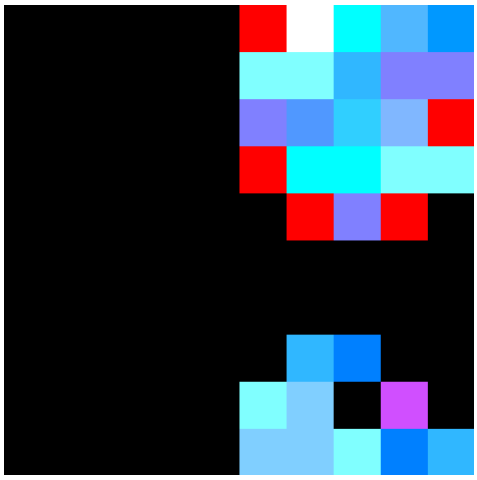

Figure 5.59. Visualisation of the Pure Kin Selection Model at Movement Probability 0.1

Figure 5.59 shows a clustered population in which uncooperative related cells (cyan) are most frequent, and uncooperative unrelated cells (blue) persist. However occasional cooperative unrelated (magenta) and cooperative related (white) cells have arisen.

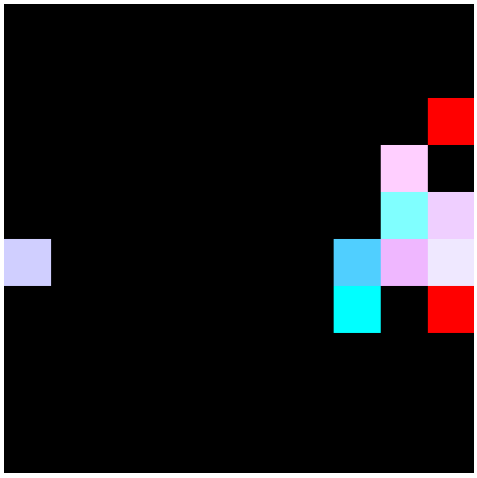

Figure 5.60. Visualisation of the Pure Kin Selection Model at Movement Probability 0.01

Figure 5.60 shows a tightly clustered population in which some uncooperative related (cyan) cells still exist, but in which cooperative unrelated (magenta) tending to cooperative related (white) cells have increased in frequency.

5.11.3 Visualisation of the Pure Reciprocal Cooperation Model

Figures 5.61 to 5.64 below present visualisations of the pure reciprocal cooperation model at movement probabilities 1, 0.5, 0.1 and 0.01 respectively.

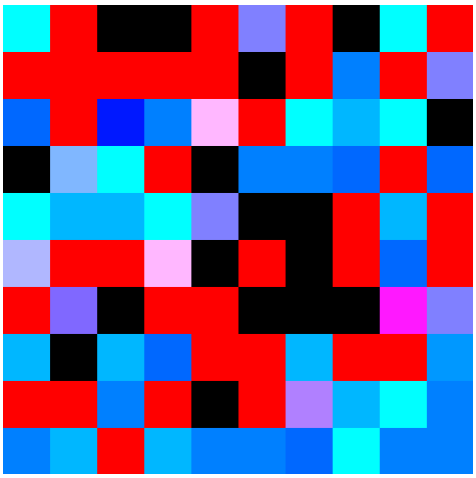

Figure 5.61. Visualisation of the Pure Reciprocal Cooperation Model at Movement Probability 1

Figure 5.61 shows a highly heterogeneous population comprised of single agent cells (red), uncooperative related cells (cyan), uncooperative unrelated cells (blue) and cooperative unrelated cells (magenta).

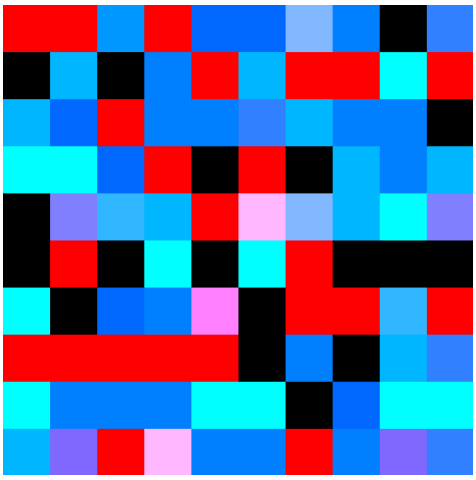

Figure 5.62. Visualisation of the Pure Reciprocal Cooperation Model at Movement Probability 0.5

Figure 5.62 shows a population that is very similar to that presented in figure 5.61 in its composition.

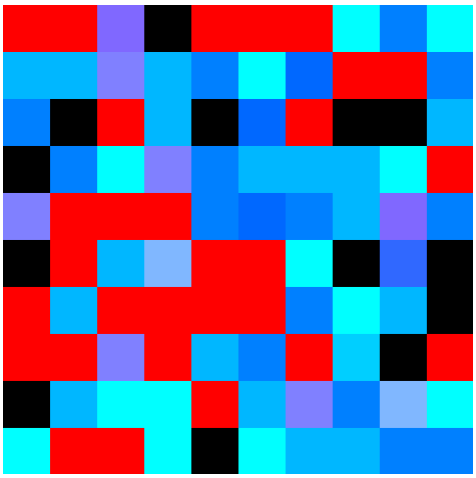

Figure 5.63. Visualisation of the Pure Reciprocal Cooperation Model at Movement Probability 0.1

Figure 5.63 shows a population in which cooperative unrelated cells (magenta) seem to have disappeared, leaving only single agent cells (red), uncooperative related cells (cyan) and uncooperative unrelated cells (blue).

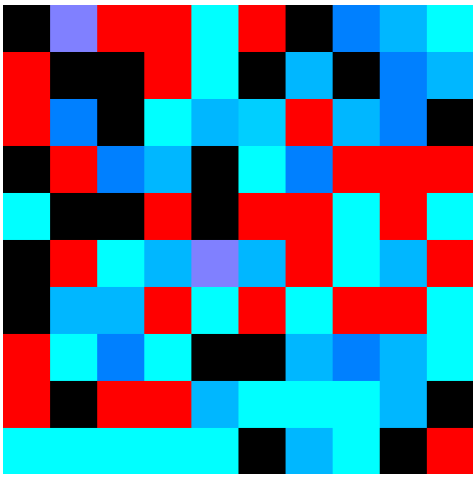

Figure 5.64. Visualisation of the Pure Reciprocal Cooperation Model at Movement Probability 0.01

Figure 5.64 presents a population in which uncooperative related cells (cyan) have increased in frequency, with occasional uncooperative unrelated cells (blue) and frequent single agent cells (red).

It should be noted that the clustering under reduced movement probability observed in the visualisations of the Evolutionary Prisoner's Dilemma and the pure kin selection model, presented in sections 5.11.1 and 5.11.2 respectively, is not observed in the visualisations of the pure reciprocal cooperation model presented here. The reason for this is the mechanism used to prevent interactions among relatives, which distributes offspring randomly within the entire environment. Therefore even under low movement probabilities in the pure reciprocal cooperation model the population will be widely distributed.

5.12 Conclusion

This chapter has presented results collected from the Evolutionary Prisoner's Dilemma, the pure kin selection model, and the pure reciprocal cooperation model described in chapters 3 and 4. Local population regulation has been investigated in both the Evolutionary Prisoner's Dilemma and the pure kin selection model. Results have also been presented on variants of the Evolutionary Prisoner's Dilemma motivated by Oliphant's (1994) model. An extended interaction length version of the Evolutionary Prisoner's Dilemma has been investigated and results presented, as have results from substituting payoffs from the Battle of the Sexes into the Evolutionary Prisoner's Dilemma. Visualisations of the Evolutionary Prisoner's Dilemma, the pure kin selection model and the pure reciprocal cooperation model have also been presented for different movement probabilities. The discussion of these results is the subject of the next chapter.

Chapter 6 – Discussion

6.1 Introduction

This chapter discusses the results from the Evolutionary Prisoner's Dilemma and the other simulation models, which were presented in chapter 5. The aim of this discussion is to gain an understanding of the behaviour of these models, and more specifically to identify the relative contribution of kin selection and repeated interaction to the cooperation observed in the Evolutionary Prisoner's Dilemma, and the ways in which they interact. This chapter is divided as follows: section 6.2 evaluates the results from the models against Hamilton's inclusive fitness rule, to assess the degree to which the Evolutionary Prisoner's Dilemma and pure kin selection model support altruism through kin selection under the parameters studied. Similarly, section 6.3 evaluates the degree to which the Evolutionary Prisoner's Dilemma and the pure reciprocal cooperation model support cooperation through repeated interaction under the parameters studied. Section 6.4 presents a comparison of some of the various results obtained from the different models in an attempt to identify the relative contributions of kin selection and repeated interaction to explaining the cooperation observed in the models, as well as investigating the interaction of the two mechanisms. Section 6.5 discusses some of the other results generated by some of the models studied, and finally section 6.6 discusses the behaviour of the models when there is no agent mobility.

6.2 The Importance of Kin Selection in the Models Studied

This section investigates the degree of support provided for kin-selected altruism in the Evolutionary Prisoner's Dilemma and pure kin selection model. These models are evaluated against Hamilton's rule for the spread of altruism under kin selection, and Hamilton's inclusive fitness rule is also applied. These investigations reveal a force opposing the operation of kin selection in the Prisoner's Dilemma and other 2 x 2 games.

6.2.1 Hamilton's Rule

Section 1.4.1 introduced kin selection theory and presented Hamilton's rule for the spread of an altruistic trait by kin selection

$$\frac{c}{b} < r$$

Hamilton's rule states that an altruistic trait can only spread by kin selection if the ratio of the cost to the donor, to the benefit to the recipient, is less than the coefficient of relationship between those two individuals. For the Evolutionary Prisoner's Dilemma the values of the cost and the benefit can be calculated from the Prisoner's Dilemma payoff matrix, and chapter 5 presented results on the coefficient of relationship between interacting individuals. Therefore it is possible to evaluate instances of the Evolutionary Prisoner's Dilemma against Hamilton's rule to determine if they support kin selection. This evaluation is also possible for the pure kin selection model.

For the Evolutionary Prisoner's Dilemma, an altruistic act is one in which an agent cooperates while its opponent defects, therefore the cost $\boldsymbol{c}$ can be calculated as the difference between the payoff the donor agent would have received if it had defected and the payoff it does receive. That is, $\boldsymbol{c} = \boldsymbol{P} - \boldsymbol{S}$. Similarly the benefit $\boldsymbol{b}$ can be calculated as the difference between the payoff the recipient agent would have received if its opponent had defected and the payoff it does receive. So $\boldsymbol{b} = \boldsymbol{T} - \boldsymbol{P}$. The cost and benefit are calculated identically for the pure kin selection model. Substituting the Prisoner's Dilemma payoffs $\boldsymbol{T} = 5$, $\boldsymbol{R} = 3$, $\boldsymbol{P} = 1$ and $\boldsymbol{S} = 0$ used to generate the results presented in chapter 5, Hamilton's rule becomes

$$\frac{1}{4} < r$$

So the coefficient of relationship $\boldsymbol{r}$ must exceed 25% in order for altruism to be favoured by kin selection in the Evolutionary Prisoner's Dilemma and pure kin selection model. A quick survey of the results from the Evolutionary Prisoner's Dilemma and the pure kin selection model, presented in sections 5.4 and 5.5 respectively, confirms that this modest requirement is amply satisfied, with relatedness levels in excess of 60% being the norm under all movement probabilities.

The calculation of the cost and benefit of "altruism" in the Battle of the Sexes can be similarly performed. So, $\boldsymbol{c} = \boldsymbol{B_B} - \boldsymbol{A_B}$ and $\boldsymbol{b} = \boldsymbol{B_A} - \boldsymbol{B_B}$ where $\boldsymbol{A_B}$ is the payoff to an individual playing A against a player choosing B, and similarly $\boldsymbol{B_A}$ and $\boldsymbol{B_B}$ are respectively the payoffs to B played against A and B played against itself. Referring to table 1.3 for these payoffs, it can be seen that $\boldsymbol{c}$ is negative, indicating that actually the "altruistic" act increases the individual fitness of the donor in the Battle of the Sexes. Thus strong altruism is not possible in the Battle of the Sexes.

6.2.2 Inclusive Fitness

It is also possible to calculate the inclusive fitness of the alleles for cooperation and defection in the Evolutionary Prisoner's Dilemma and pure kin selection model. In the following equations from Marshall & Rowe (2000), $\boldsymbol{T}$, $\boldsymbol{R}$, $\boldsymbol{P}$ and $\boldsymbol{S}$ represent the payoffs in the Prisoner's Dilemma, $\boldsymbol{r}$ is the average coefficient of relationship in the population at the altruistic locus, and $\boldsymbol{f_c}$ is the frequency of cooperative alleles in the environment at a related locus. Then the inclusive fitness of a cooperation allele is

$$i_c = (Rf_c + S(1 - f_c)) + (r(Rf_c + T(1 - f_c)))$$

Similarly the inclusive fitness of a defection allele is

$$i_d = (Tf_c + P(1 - f_c)) + (r(Sf_c + P(1 - f_c)))$$

In each of these equations the first term represents the individual fitness of the allele in the interacting individual carrying that allele, while the second term represents the individual fitness of a copy of that allele in the other interacting individual, weighted by the coefficient of relationship $\boldsymbol{r}$. This is the standard inclusive fitness calculation (Hamilton, 1964a), interpreting payoff from a Prisoner's Dilemma interaction as reproductive potential. Each fitness term is the expected payoff received by one of the interacting individuals weighted by the probability $\boldsymbol{f_c}$ that any encountered individual will cooperate in such an interaction.

These equations were used to calculate the relative inclusive fitness of alleles for cooperation (C) and defection (D) at different degrees of relatedness and frequencies of cooperative alleles, presented in Marshall & Rowe (2000) and reproduced below in figure 6.1. The Prisoner's Dilemma payoffs used in this calculation were $\boldsymbol{T} = 5$, $\boldsymbol{R} = 3$, $\boldsymbol{P} = 1$ and $\boldsymbol{S} = 0$.

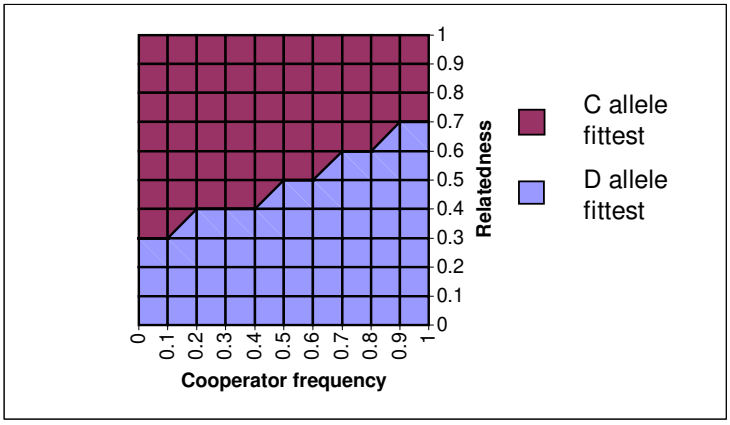

Figure 6.1. Relative Inclusive Fitness of Cooperation and Defection Alleles

Figure 6.1 reveals a more complicated picture than that given by Hamilton's rule alone, which predicts that altruistic behaviour will be favoured when the coefficient of relationship exceeds 25%. Figure 6.1 shows that the relative inclusive fitness of the alleles for cooperation and defection is actually dependent on the frequency of cooperation alleles in the environment, as well as the coefficient of relationship. It should be noted that frequency of cooperation alleles used here is actually the frequency of cooperation alleles at a locus other than the altruistic locus, so the degree of relatedness at the altruistic locus is independent of this frequency. The reasons that the frequency of cooperation alleles at a locus other than the altruistic locus is significant were explained in detail in section 3.3.2. Briefly, when using two-dimensional strategies in a 2 x 2 game such as the Prisoner's Dilemma, altruism is only possible when the two individuals use different loci to determine their next action based on their interaction history together, namely the merciful / exploitative and the forgiving / vengeful loci in the case of the Prisoner's Dilemma. Then one individual can only perform an altruistic act if it has a cooperation allele at the locus it uses to determine its current action, while the other individual has a defection allele at the locus it determines its current action with. Given this fact, it can be seen that the inclusive fitness calculation for altruism at such a locus is dependent not only on the degree of relatedness at that locus, but also the frequency of cooperation and defection alleles at the other locus.

Figure 6.1 shows that as the frequency of cooperation alleles increases in the population, the degree of relatedness at which altruism is favoured increases. It is possible to calculate the relatedness threshold above which altruism will be favoured by kin selection for different cooperation allele frequencies. The relatedness threshold is at the point $\boldsymbol{i_c = i_d}$. This can be rearranged such that the relatedness threshold is given by

$$r' = \frac{(Tf_c + P(1 - f_c)) - (Rf_c + S(1 - f_c))}{(Rf_c + T(1 - f_c)) - (Sf_c + P(1 - f_c))}$$

Figure 6.2 below presents the relatedness threshold for the full range of cooperation allele frequencies.

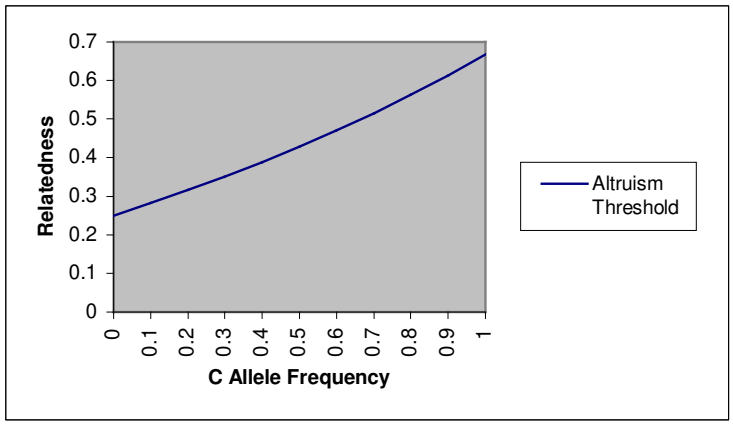

Figure 6.2. Relatedness Threshold for Altruism Favoured by Kin Selection

When there are no cooperation alleles in the environment, the degree of relatedness at which altruism is favoured is that predicted by Hamilton's rule. That is $i_c = i_d$ when $f_c = 0$ and $r = 0.25$. However, when there are no defection alleles in the environment, the relatedness threshold is substantially increased, so $i_c = i_d$ when $f_c = 1$ and $r = 0.67$. The average level of relatedness in the pure kin selection model is still significantly above this threshold, at around 80%. However the average relatedness in the Evolutionary Prisoner's Dilemma is much closer to the threshold, at around 70%. The implication of this is that kin selection may be a weak selective force on cooperation in the Evolutionary Prisoner's Dilemma, if the frequency of cooperation alleles approaches 1. However a note of caution must be sounded with regard to the interpretation of relatedness results from the model when considering the altruism threshold. This is due to the way in which relatedness is calculated, which may mean that highly related individuals are related for either cooperation or defection alleles. Obviously this could lead to an incorrect value of the relatedness r required for the calculation of the inclusive fitness of cooperation and defection alleles, so relatedness results from the model cannot be used to accurately assess the altruism threshold in the model. Additionally, while relatedness measure $\overline{r_2}$ measures relatedness on the loci subject to kin selection for altruism, this relatedness is a combination of the relatedness at loci that may potentially have very different degrees of relatedness. This also means that relatedness results from the model cannot be used to accurately predict the altruism threshold in the model. In order to overcome these problems, a new measure of relatedness needs to be developed which distinguishes between relatedness for cooperation alleles and relatedness for defection alleles, as well as separately calculating the relatedness at each of the loci subject to kin selection for altruism.

6.2.3 A Force Opposing Kin Selection for Altruism in the Prisoner's Dilemma

That the strength of kin selection for altruism in the Evolutionary Prisoner's Dilemma is weakened by an increase in the frequency of cooperation alleles, as identified in the preceding section, is particularly

relevant as the operation of kin selection at the two loci subject to kin selection for altruism, namely the merciful / exploitative and forgiving / vengeful loci, is symmetric. That is to say that kin selection can operate equally on both of these loci, and the operation of kin selection at each of these loci involves the other. However, as kin selection at one of these loci is weakened by an increase in the frequency of cooperation alleles at the other locus, the increase of alleles for cooperation at either locus through kin selection will hinder the operation of kin selection at the other locus. To put it another way, the success of kin selection at one locus will undermine the efficacy of kin selection at the other locus, and vice versa. It is important to note that this effect is not limited to the Prisoner's Dilemma, but includes any 2 x 2 game in which individuals use different loci to determine their actions in the game.

6.3 The Importance of Reciprocal Cooperation in the Models Studied

This section evaluates the support for cooperation through repeated interaction provided by the Evolutionary Prisoner's Dilemma and the pure reciprocal cooperation model. The models are evaluated against Axelrod's (1984) condition for the collective stability of Tit-for-Tat, and a mathematical model of expected interaction length in the models is considered. The results of the investigation motivate the study of a variant of the Evolutionary Prisoner's Dilemma in which the number of interactions between agents at each meeting is increased.

6.3.1 The Collective Stability of Tit-for-Tat

In section 1.3.2 the significance of the discount parameter w, also known as the "shadow of the future", was introduced. A more detailed investigation of the significance of w for reciprocal cooperation was presented by Axelrod (1984), who proved that the strategy Tit-for-Tat is collectively stable only if

$$w > \max[(T-R)/(T-P), (T-R)/(R-S)]$$

where `max` evaluates to the larger of the two values in brackets. This can be broken down into two separate requirements. The first requirement $w > (T - R) / (T - P)$ is the requirement that Tit-for-Tat cannot be invaded by the strategy of unconditional defection, All-D. The second requirement $w > (T - R) / (R - S)$ is the requirement that Tit-for-Tat cannot be invaded by the strategy that alternates defection with cooperation, which shall be called Alternating-D-C for the purposes of this discussion. These two strategies were determined by Axelrod to be the two representative strategies against which Tit-for-Tat should be tested for collective stability.

The reciprocal cooperative strategy Tit-for-Tat is one of the most robust and successful strategies in the Prisoner's Dilemma without noise (Axelrod, 1984), which is the interaction model used in the Evolutionary Prisoner's Dilemma. Therefore Axelrod's condition for the collective stability of Tit-for-Tat is used here as a guide to assessing the degree to which reciprocal cooperation is supported in the Evolutionary Prisoner's Dilemma under the parameters studied.

The Evolutionary Prisoner's Dilemma uses two-dimensional strategies for each of its agents. Tit-for-Tat and All-D are easy to represent in a general form as one-dimensional or two-dimensional strategies. The

strategy Alternating-D-C, however, can only be represented as a two-dimensional strategy, as shown in table 6.1 below.

Previous actions agent / opponent	**Current action**
Initial action	D
C / C	D
D / C	C
C / D	D
D / D	C

Table 6.1. A Two-Dimensional Strategy to Alternate Defection with Cooperation

Evaluating Axelrod's condition for the collective stability of Tit-for-Tat, using the Prisoner's Dilemma payoffs $\boldsymbol{T} = 5$, $\boldsymbol{R} = 3$, $\boldsymbol{P} = 1$ and $\boldsymbol{S} = 0$ from the Evolutionary Prisoner's Dilemma, gives the following conditions

$\boldsymbol{w} > 0.5$ for the collective stability of Tit-for-Tat against All-D

$\boldsymbol{w} > 0.67$ for the collective stability of Tit-for-Tat against Alternating-D-C

The discount parameter $\boldsymbol{w}$ is equivalent to the probability that, given one interaction between two individuals, there will be another interaction between those same individuals. Data on the probability of continued interaction were not collected from the Evolutionary Prisoner's Dilemma and other models, however data on the average number of interactions were. Interaction between individuals is a geometric process, so the expected number of interactions between two individuals can be calculated as $\boldsymbol{i} = 1 / (1 - \boldsymbol{w})$. This means that the minimum number of interactions required for the stability of Tit-for-Tat against All-D is 2, while for stability against Alternating-D-C the minimum number of interactions required is 3. The minimum number of interactions required for the collective stability of Tit-for-Tat is therefore 3.

An examination of the results presented in chapter 5 shows that the average number of interactions in the Evolutionary Prisoner's Dilemma and pure reciprocal cooperation model rarely reaches 3 in any of the cases studied. In the results from the Evolutionary Prisoner's Dilemma presented in section 5.4.2, the average number of interactions only reaches 1.5 at its highest point. The Evolutionary Prisoner's Dilemma with local population regulation in section 5.7.2 shows an increased average number of interactions, as does the Evolutionary Prisoner's Dilemma with defector-disadvantageous payoffs studied in section 5.8.1. However the average number of interactions in both these model configurations still stays below 3, but above 2, at their highest points. In the pure reciprocal cooperation model, presented in section 5.6.2, the average number of interactions is also higher, but still only reaches 2.5 at its highest. It is only in the pure reciprocal cooperation model with long agent lifespan, presented in section 5.6.3, that the average number of interactions finally exceeds 3 at its high point, reaching 4 at movement probability 0. In all the cases described above, the average number of interactions has very little variance, with a typical standard deviation of less than ten percent.

6.3.2 A Mathematical Model of Expected Interaction Length

The failure of the Evolutionary Prisoner's Dilemma to provide full support for reciprocal cooperation under the parameters studied is important. A parameter configuration that provides stronger support for reciprocal cooperation is desirable, however this can be shown to be problematic. Marshall & Rowe (2000) presented a model of the probability of two consecutive interactions between the same agents in the Evolutionary Prisoner's Dilemma, the construction of which is presented here. In the following equations, ***d*** is the environmental death probability, ***m*** is the agent movement probability, and $\overline{p}$ is the average cell population size for populated cells.

As cells are used as the local area for interaction, in order for two agents who interact in one timestep to interact in the following timestep, both must end up occupying the same cell in the environment. As the agents interacted in the first place they are necessarily in the same cell to begin with. Then there are two possible ways in which they can end up occupying the same cell in the following timestep: both agents can remain in the same cell, or both agents can move to the same neighbouring cell. Therefore the probability of both agents ending up in the same cell on the next timestep is

$$(1-m)^2 + \frac{m^2}{8}$$

where the first term corresponds to the probability that both agents remain in the same cell, and the second term corresponds to the probability that both agents move to the same cell in their Moore neighbourhood of eight cells.

Assuming that both agents end up in the same cell, in order to interact both agents must survive the random death in the environment, and must also be formed into an interaction pair during the random process of pairing agents in a cell's population. Thus the probability of both agents interacting together once they are in the same cell is

$$\frac{(1-d)^2}{\overline{p}-1}$$

Then given one interaction between a pair of agents, the probability that the same pair of agents will interact on the following timestep is

$$u = \frac{(1-d)^2}{\overline{p}-1}\left((1-m)^2 + \frac{m^2}{8}\right)$$

The probability of repeated interaction given by ***u*** is a simplification of that actual probability in two respects. Firstly, it ignores the possibility of agent death through lack of energy, which occurs when an agent is unable to generate enough energy from its interactions with other agents to cover the environmental cost of living. Taking account of this possibility is very difficult and for simplicity it is ignored here. Secondly, the calculation of ***u*** does not account for the possibility of agents interacting again at some timestep in the future other than the next timestep. Taking account of this possibility

becomes more complicated the more timesteps in the future are considered in calculating the repeated interaction probability, and again for simplicity it is ignored here. The importance of these simplifications will be considered later.

As discussed earlier, interaction between individuals is a geometric process, so given the repeated interaction probability $\boldsymbol{u}$ the expected number of interactions is $\boldsymbol{v} = 1 / (1 - \boldsymbol{u})$. The environmental death probability $\boldsymbol{d}$ and the movement probability $\boldsymbol{m}$ are specified by the environment, however the average cell population size $\overline{p}$ is collected from simulation runs as described in section 5.2.5. Calculating $\boldsymbol{v}$ for values of $\boldsymbol{d}$, $\boldsymbol{m}$, and $\overline{p}$ from the Evolutionary Prisoner's Dilemma presented in section 5.4 gives figure 6.3 below, to which the empirical average number of interactions collected from the model has been added for comparison.

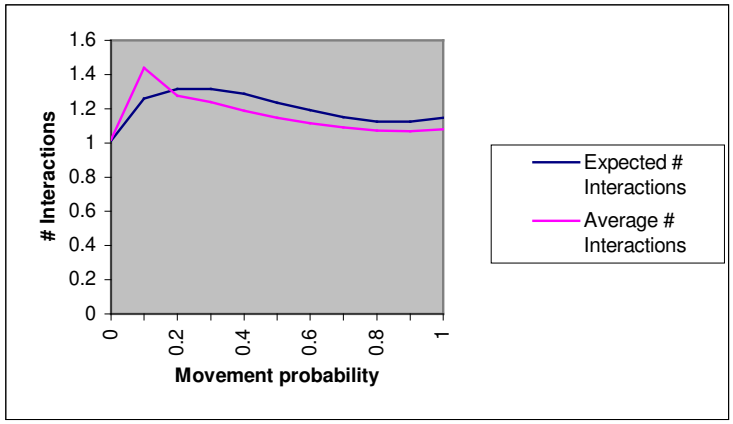

Figure 6.3. Expected Number of Interactions in the EPD

As can be seen from figure 6.3, the expected number of interactions gives a reasonably good approximation of the average number of interactions in the Evolutionary Prisoner's Dilemma, although it does overestimate the expected number of interactions at all except the lowest movement probabilities.

Figure 6.4 below presents $\boldsymbol{v}$ calculated using values of $\boldsymbol{d}$, $\boldsymbol{m}$, and $\overline{p}$ from the pure reciprocal cooperation model with long agent lifespan presented in section 5.6.3.

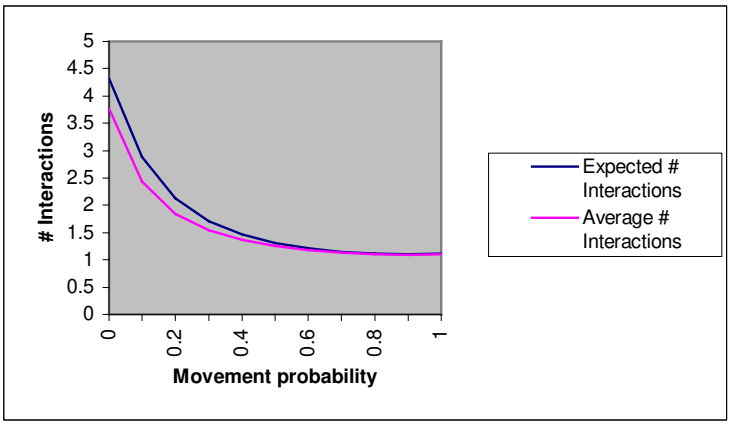

Figure 6.4. Expected Number of Interactions in the Pure Reciprocal Cooperation Model with Long Agent Lifespan

Figure 6.4 shows that the expected number of interactions also gives a good approximation of the average number of interactions in the pure reciprocal cooperation model with long agent lifespan, although it slightly overestimates the expected number of interactions at the lower movement probabilities.

Figure 6.5 below presents the expected number of interactions for the pure reciprocal cooperation model presented in section 5.6.2.

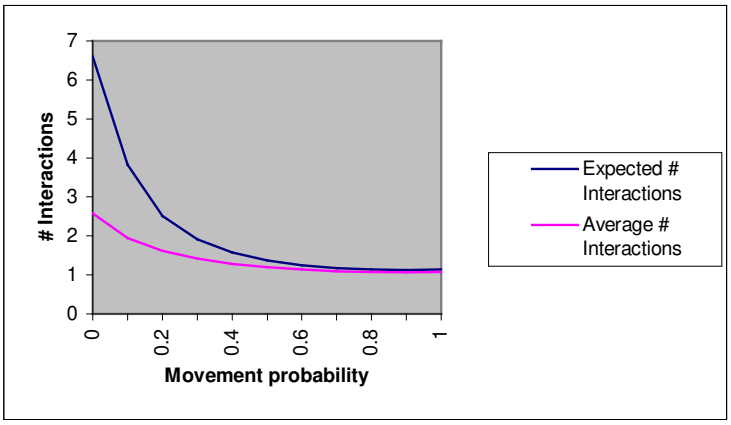

Figure 6.5. Expected Number of Interactions in the Pure Reciprocal Cooperation Model

As can be seen in figure 6.5, the expected number of interactions becomes increasingly inaccurate as movement probability decreases. At movement probability 0 the expected number of interactions is more than double the actual average number of interactions.

The purpose of this investigation into the expected number of interactions in the Evolutionary Prisoner's Dilemma and pure reciprocal cooperation model has been twofold. Firstly it has highlighted assumptions in the model that were not sufficiently considered in Marshall & Rowe (2000). The result of these assumptions can be a significant divergence of the expected number of interactions from the average number of interactions collected from simulation runs. That cases exist where such large divergences occur severely limits the usefulness of the expected number of interactions formula when investigating

models based on the Evolutionary Prisoner's Dilemma. The second purpose of the investigation runs counter to the conclusion of the first, as it uses the expected number of interactions formula to investigate what parameters may support reciprocal cooperation in the Evolutionary Prisoner's Dilemma. Although the expected number of interactions can diverge significantly from the average number of interactions determined empirically, in the case presented above in figure 6.5 where it diverges most significantly, the expected number of interactions overestimates the actual number of interactions. In the other cases presented in figures 6.3 and 6.4, the expected number of interactions predicts the average number of interactions quite well, although again it is typically an overestimate. In fact, of all three cases presented above, there is only one movement probability in one case at which the expected number of interactions proves to be an underestimate of the average number of interactions. The observation that the expected number of interactions is typically an overestimate of the average number of interactions will be used in the next section to show that an average number of interactions large enough to support reciprocal cooperation is difficult to obtain in the Evolutionary Prisoner's Dilemma. More importantly, the expected number of interactions formula will also be used as a heuristic in the next section, to provide intuitions into the operation of repeated interaction in certain classes of viscous population.

6.3.3 Conditions Which Favour Reciprocal Cooperation

As discussed above, the collective stability requirement for Tit-for-Tat using the Prisoner's Dilemma payoffs from the Evolutionary Prisoner's Dilemma is for an average number of interactions of at least 3. This section will use the repeated interaction probability $\boldsymbol{u}$ from Marshall & Rowe (2000) to assess the degree of support for reciprocal cooperation in the Evolutionary Prisoner's Dilemma. Although the repeated interaction probability formula is flawed, as discussed in the preceding section, it can still provide a useful guide to whether a given parameter configuration of the Evolutionary Prisoner's Dilemma will provide suitable conditions for reciprocal cooperation.

The expected number of interactions is given by $\boldsymbol{v} = 1 / (1 - \boldsymbol{u})$ which, after substituting in the full expression for $\boldsymbol{u}$, given in the preceding section, and some rearrangement, gives the requirement for the average local cell population

$$\bar{p}' = (1-d)^2 \div \left(\frac{1 - \frac{1}{v}}{(1-m)^2 + \frac{m^2}{8}} \right) + 1$$

Taking the requirement for the collective stability of Tit-for-Tat as the expected number of interactions gives $\boldsymbol{v} = 3$. Then, with death probability $\boldsymbol{d} = 0.05$ from the Evolutionary Prisoner's Dilemma the formula above can be used to calculate the maximum average local population size required for the collective stability of Tit-for-Tat under varying movement probability, as shown below in figure 6.6.

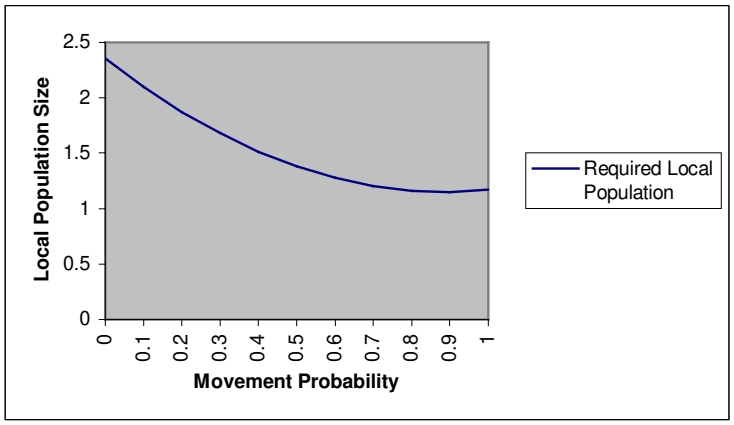

Figure 6.6. Maximum Local Population Size Required for Collective Stability of Tit-for-Tat in the EPD

Figure 6.6 shows that the maximum average local population size required to make Tit-for-Tat collectively stable is very low, below 2 at most movement probabilities. The situation is not significantly improved by reducing the death probability ***d*** to 0. A local population size of 2 is the minimum required for interaction to occur within the Evolutionary Prisoner's Dilemma, as two agents must inhabit the same cell if they are to interact. This fact, coupled with the requirement for agents to interact regularly in order to survive, means that an average local population size of around or below 2 is close to the minimum level required for agents to survive in the model. This, taken together with the observation that the expected number of interactions ***v*** is typically an over-optimistic estimate of the actual number of interactions, as noted in the previous section, suggests that finding a parameter configuration that supports the collective stability of Tit-for-Tat in the Evolutionary Prisoner's Dilemma will be very difficult. This suggestion is supported by the results on average number of interactions presented in the previous chapter, in which the average number of interactions very rarely reaches the level that the collective stability of Tit-for-Tat requires.

It is possible to generalise this result to a result for viscous populations in which increased viscosity also leads to an increase in the local population density experienced by individuals in that population, of which the Evolutionary Prisoner's Dilemma is an example. To do this it is necessary to treat the expected number of interactions formula presented above as a heuristic for the actual number of interactions in the population. The expected number of interactions formula gives an indication of the probability of another interaction between two individuals in the next timestep, given they interact in the current timestep. Intuitively, if this probability is increased, then the probability of a future interaction between the same two individuals at any timestep in the future is also increased. The expected number of interactions formula has been used to calculate the maximum average local population size required for the collective stability of Tit-for-Tat, presented in figure 6.6 above. As can be seen from figure 6.6, the maximum average local population size required for the collective-stability of Tit-for-Tat increases as movement probability decreases. At the same time, viscous populations such as the Evolutionary Prisoner's Dilemma exhibit an increase in average local population size as movement probability decreases. The question of how much support is provided for reciprocal cooperation in such a viscous population

therefore rests on the relative rates of increase of the average local population size, and of the maximum local population size required for the collective stability of Tit-for-Tat, as movement probability decreases.

6.3.4 A Variant on the Evolutionary Prisoner's Dilemma

One of the conclusions of the previous section, that the Evolutionary Prisoner's Dilemma is very unlikely to provide the conditions for the collective stability of Tit-for-Tat, and hence for reciprocal cooperation to be favoured, motivated the design and study of a variant of the Evolutionary Prisoner's Dilemma presented in section 5.9. The extended length Evolutionary Prisoner's Dilemma has a modified method of interaction between agents, in which a pair of agents interacting on one timestep play an iterated Prisoner's Dilemma of three rounds, with prior history. This corresponds to Axelrod's (1984) proposal for promoting cooperation by making interactions more durable.

A comparison of the results from the Evolutionary Prisoner's Dilemma both with and without extended interaction length, presented in sections 5.9.2 and 5.4.2 respectively, shows that both average number of interactions and cooperation level are increased by extending the interaction length, as expected. The average number of interactions in the Evolutionary Prisoner's Dilemma with extended interaction length, presented in figure 5.49, is increased to approximately 5 at movement probability 0.1, compared with an average number of interactions of 1.5 for the standard Evolutionary Prisoner's Dilemma with the same movement probability, presented in figure 5.8. This increase is slightly more than is expected by simply multiplying the average number of interactions from the standard Evolutionary Prisoner's Dilemma by three. The increase in average number of interactions corresponds to an increase in the average cooperation level in the Evolutionary Prisoner's Dilemma with extended interaction length, presented in figure 5.48, when compared with the standard Evolutionary Prisoner's Dilemma, presented in figure 5.5. This increase is most pronounced at low movement probabilities, where the cooperation level in the Evolutionary Prisoner's Dilemma with extended interaction length typically exceeds 70%, compared with approximately 50% in the standard Evolutionary Prisoner's Dilemma. The observation that an increased average number of interactions in the Evolutionary Prisoner's Dilemma corresponds with an increased average cooperation level provides evidence that repeated interaction is a significant factor in explaining observed cooperation in the model.

Comparing the average cooperation level and average number of interactions for the Evolutionary Prisoner's Dilemma with extended interaction length, presented in figures 5.48 and 5.49 respectively, cooperation levels in excess of 50% correspond with an average number of interactions of 4 or above. This suggests that the condition for the collective stability of Tit-for-Tat may not be the most appropriate condition to use for evaluating the degree of support for reciprocal cooperation in a model, as it was presented in section 6.3.1. Rather, the condition for invasion of All-D by Tit-for-Tat

$$pV\langle A|A\rangle + (1-p)V\langle B|B\rangle > (1-p)V\langle B|B\rangle$$

may be more suitable, where ***A*** represents Tit-for-Tat, ***B*** represents All-D and ***p*** represents the proportion of interactions that a Tit-for-Tat player has with other Tit-for-Tat players (Axelrod, 1984). Remembering

that the expected payoff ***V*** of a strategy played against another strategy is a function of the payoffs of the game and the shadow of the future ***w***, the above condition can be used to determine the magnitude of ***w*** required for Tit-for-Tat to be able to invade All-D given some level of clustering ***p***. Unfortunately the degree of clustering of Tit-for-Tat in the model is unknown, and as no equation can be solved for two unknowns, the shadow of the future required for the invadability of All-D by Tit-for-Tat cannot be determined. However it can be seen that increasing the shadow of the future, which increases the payoff of Tit-for-Tat against itself faster than it increases the payoff of All-D against itself, will decrease the degree of clustering necessary for Tit-for-Tat to invade All-D. It is expected that an average number of interactions of 4 or above, as seen at low movement probabilities in the extended interaction length Evolutionary Prisoner's Dilemma, decreases the degree of clustering necessary for reciprocating strategies such as Tit-for-Tat to invade the population to that experienced in the model, giving rise to the high levels of cooperation observed.

6.4 Discussion of the Contributions of Kin Selection and Repeated Interaction to Observed Cooperation

This section attempts to assess the relative contributions of kin selection and repeated interaction to observed cooperation in the Evolutionary Prisoner's Dilemma, through investigation of the results presented in chapter 5 from the Evolutionary Prisoner's Dilemma, the pure kin selection model and the pure reciprocal cooperation model.

6.4.1 Definition of Correlation Calculations

In the course of the investigation carried out in this section correlations will be calculated to assess the relationship of results, therefore a definition is provided below for the two different methods used to calculate these correlations. For both these methods correlation is calculated as the covariance of two data sets divided by the product of their standard deviations, where covariance is the mean product of the deviations of the data points from their respective means, so

$$\rho_{X,Y} = \frac{\mathrm{cov}(X,Y)}{\sigma_X . \sigma_Y}$$

$$\mathrm{cov}(X,Y) = \frac{1}{n}\sum_{i=0}^{n}(x_i - \mu_x)(y_i - \mu_y)$$

For any experiment let X_m be the set of value pairs from all simulation runs of that experiment where the movement probability is ***m***, so $X_m = \{\{a_1, b_1\},...,\{a_{x_m}, b_{x_m}\}\}$ where $x_m \geq 1$ is the number of simulation runs carried out at movement probability ***m***, and each $\{a,b\} \in X_m$ is a pair of values from the experiment to be used in calculating a correlation. Then let $\overline{X}$ be the set of all value pairs from all simulation runs at all movement probabilities studied in that experiment, so if movement probabilities 0 to 1 are studied at interval 0.1 then $\overline{X} = X_0 \cup X_{0.1} \cup ... \cup X_1$.

It is thus possible to calculate correlations either on a single set of value pairs from all the simulation runs at a single movement probability, or on the complete set of value pairs from all the simulation runs at all movement probabilities studied. Calculating correlations on value pairs from all the movement probabilities studied allows a general correlation to be calculated between two values, while calculating correlations only on value pairs from a single movement probability allows more detailed investigations in cases where the behaviour of the model changes as movement probability changes. Such cases could lead to an impression of reduced correlation if only the correlation across all movement probabilities were considered.

The calculation of correlation on all value pairs from all movement probabilities studied shall be designated $\boldsymbol{x}$ and the correlation on value pairs only from simulation runs at a specified movement probability shall be designated $\boldsymbol{x}'$.

It is also possible to calculate the correlation between the same value, such as the average cooperation level, in two different experiments. Let $\boldsymbol{X}'$ be the set of all pairs of values taken from two experiments being compared, where the first value in a pair is the average of some value for all simulation runs at the same movement probability in one of the experiments being compared, and the second value in the pair is the average of the same value in the other experiment for all simulation runs at that same movement probability, so that if two experiments are being compared for movement probabilities 0 to 1 at interval 0.1 then $X' = \{\{a_0, b_0\}, \{a_{0.1}, b_{0.1}\}, ..., \{a_1, b_1\}\}$. The calculation of correlation between experiments in this manner shall be designated $\boldsymbol{x}''$.

6.4.2 Investigation of Results from the Evolutionary Prisoner's Dilemma

The starting point for this investigation is the results from the Evolutionary Prisoner's Dilemma, presented in section 5.4.2. A brief examination of the results for average cooperation level, average relatedness on loci subject to kin selection for altruism, and average number of interactions, presented in figures 5.5, 5.7 and 5.8 respectively, shows some similarities under varying movement probabilities. The degree of this similarity can be determined by calculating the correlation $\boldsymbol{x}$ of these results with each other. Table 6.2 below presents these correlations, calculated on all the data used to produce each of the figures 5.5, 5.7 and 5.8, so the correlations are calculated on the data from 11 different movement probabilities, with 20 simulation runs at each movement probability.

Data	Correlation
Average cooperation / average relatedness at loci subject to kin selection	0.583237
Average cooperation / average number of interactions	0.650125
Average relatedness at loci subject to kin selection / average number of interactions	0.618621

Table 6.2. Correlation of Results in the Evolutionary Prisoner's Dilemma

As can be seen from table 6.2, the correlation of average cooperation with average number of interactions in the Evolutionary Prisoner's Dilemma is the highest of those correlations presented. The scatter plot of the data used to calculate that correlation is presented below in figure 6.7.

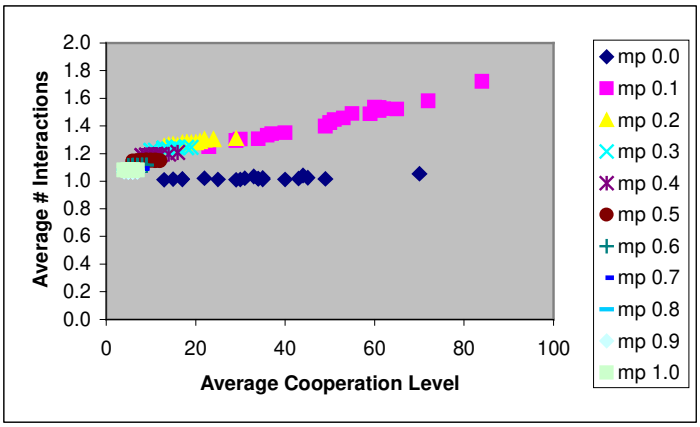

Figure 6.7. Scatter Plot of Average Cooperation Against Average Number of Interactions in the EPD at Movement Probabilities 0 to 1 with Interval 0.1

Of the three correlations presented in table 6.2, the scatter plot produced by plotting average cooperation against average number of interactions, as in figure 6.7, is the most informative. It is also informative to investigate the correlation of average cooperation with average number of interactions in more depth, by calculating the correlation of these two values separately for each movement probability studied. Therefore table 6.3 below calculates the correlation x' of average cooperation with average number of interactions at each movement probability separately, in each case using data from the 20 simulation runs performed at that movement probability.

Movement probability	Correlation
0	0.677863
0.1	0.989313
0.2	0.945298
0.3	0.890432
0.4	0.84943
0.5	0.648765
0.6	0.574599
0.7	0.103819
0.8	0.357592
0.9	0.051041
1	-0.010423

Table 6.3. Correlation of Average Cooperation with Average Number of Interactions at Different Movement Probabilities in the EPD

As can be seen from table 6.3, the highest correlation between average cooperation and average number of interactions occurs at movement probability 0.1, where the correlation is very high at 0.989313. Figure 6.8 below presents the scatter plot of average cooperation against average number of interactions at this movement probability.

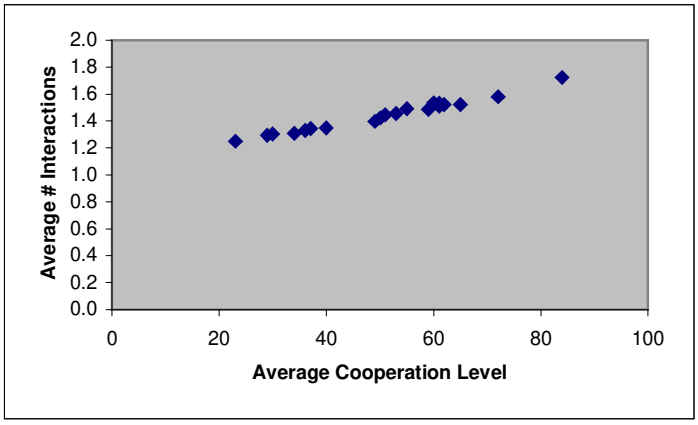

Figure 6.8. Scatter Plot of Average Cooperation Against Average Number of Interactions in the EPD at Movement Probability 0.1

Neither average cooperation against average relatedness, nor average relatedness against average number of interactions, exhibit such high degrees of correlation at any movement probability, therefore they are not presented here.

6.4.3 Investigation of Results from the Evolutionary Prisoner's Dilemma with Local Population Regulation

The results from the Evolutionary Prisoner's Dilemma with local population regulation, presented in section 5.7.2, are different from the results for the standard Evolutionary Prisoner's Dilemma, presented in section 5.2.4. The introduction of local population regulation has had the effect of reducing the average cooperation level at all movement probabilities except movement probability 0. At movement probability 0, the cooperation level is higher with local population regulation than without, and this has removed the discontinuity between cooperation levels at movement probability 0 and 0.1 that is characteristic of the standard Evolutionary Prisoner's Dilemma.

The results from the Evolutionary Prisoner's Dilemma with local population regulation show some similarities in the behaviour over varying movement probability of the average cooperation level, average relatedness level and average number of interactions, presented in figures 5.32, 5.33 and 5.34 respectively. Table 6.4 below presents the correlation $\boldsymbol{x}$ of each of these values against the others, calculated for all the simulation runs at all movement probabilities studied.

Data	Correlation
Average cooperation / average relatedness at loci subject to kin selection	0.943316
Average cooperation / average number of interactions	0.971667
Average relatedness at loci subject to kin selection / average number of interactions	0.974616

Table 6.4. Correlation of Results in the Evolutionary Prisoner's Dilemma with Local Population Regulation

As can be seen from table 6.4, average cooperation level, average relatedness level and average number of interactions are all highly correlated with each other in the Evolutionary Prisoner's Dilemma with local population regulation. These correlations are higher than those found in the standard Evolutionary Prisoner's Dilemma and presented in section 6.4.2. Figures 6.9 to 6.11 below show the scatter plots for all simulation runs at all movement probabilities for each of the correlations presented in table 6.4.

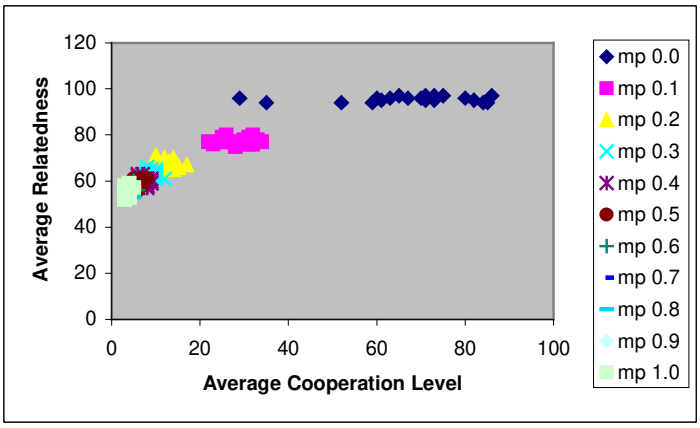

Figure 6.9. Scatter Plot of Average Cooperation Against Average Relatedness in the EPD with Local Population Regulation at Movement Probabilities 0 to 1 with Interval 0.1

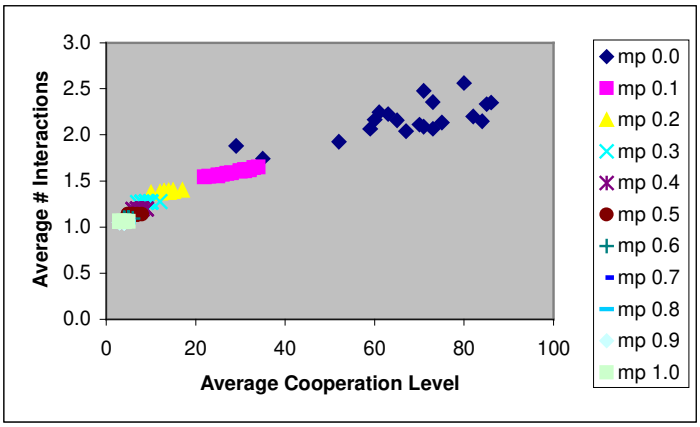

Figure 6.10. Scatter Plot of Average Cooperation Against Average Number of Interactions in the EPD with Local Population Regulation at Movement Probabilities 0 to 1 with Interval 0.1

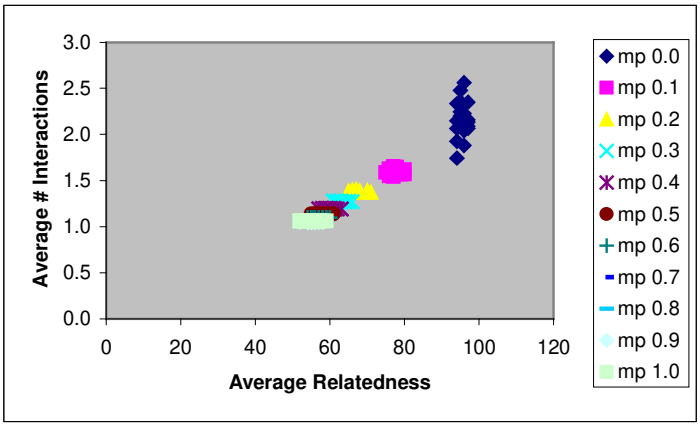

Figure 6.11. Scatter Plot of Average Relatedness Against Average Number of Interactions in the EPD with Local Population Regulation at Movement Probabilities 0 to 1 with Interval 0.1

The relatedness measure used in figures 6.9 and 6.11 is measure $\bar{r}_2$, which calculates relatedness only on the loci subject to kin selection.

Table 6.5 presents the correlation x' of average cooperation with average number of interactions, calculated separately for each of the movement probabilities studied.

Movement probability	**Correlation**
0	0.724928
0.1	0.98425
0.2	0.912892
0.3	0.790227
0.4	0.518233
0.5	0.08186
0.6	0.109763
0.7	0.346302
0.8	-0.018525
0.9	0.05
1	-0.349201

Table 6.5. Correlation of Average Cooperation with Average Number of Interactions at Different Movement Probabilities in the EPD with Local Population Regulation

Table 6.5 shows a high degree of correlation between average cooperation and average number of interactions at movement probabilities 0 to 0.3, then no significant correlations at higher movement probabilities.

Calculating the correlation x' of average cooperation with average relatedness at loci subject to kin selection for each movement probability reveals no significant correlations. The same is true for the correlation x' of average relatedness at loci subject to kin selection with average number of interactions.

6.4.4 Comparison of Results from the Evolutionary Prisoner's Dilemma with Results from the Pure Kin Selection Model

A comparison of the average cooperation level in the Evolutionary Prisoner's Dilemma with the average cooperation level in the pure kin selection model, presented in figures 5.5 and 5.16 respectively, also reveals similar behaviour. This can be quantified by calculating the correlation x'' of the cooperation level in both models, averaged over all simulation runs at each movement probability. The average cooperation levels in the two models are very well correlated at 0.987301. The corresponding scatter plot is presented below in figure 6.12.

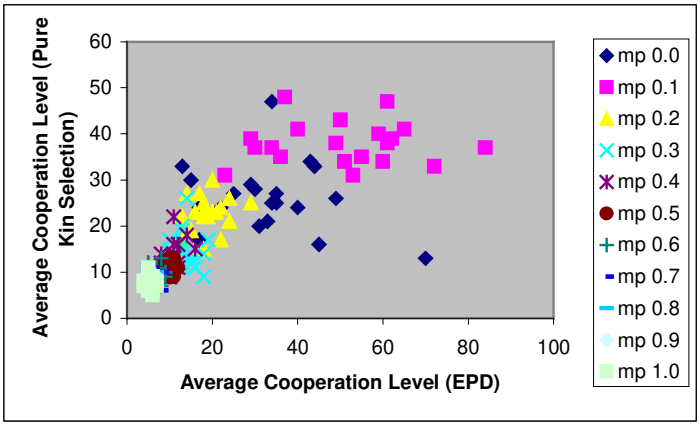

Figure 6.12. Scatter Plot of Average Cooperation in the EPD Against Average Cooperation in the Pure Kin Selection Model at Movement Probabilities 0 to 1 with Interval 0.1

6.4.5 Investigation of Results from the Pure Kin Selection Model

An examination of the results from the pure kin selection model presented in section 5.5.2 shows that the behaviour of the average cooperation level and the average relatedness level, presented in figures 5.16 and 5.17 respectively, seems to have some kind of relationship. In fact the cooperation level and relatedness level are inversely correlated, with a correlation of –0.671319. As in the preceding sections, the correlation x is calculated on the results of all the simulation runs at all the movement probabilities. The scatter plot of average cooperation level against average relatedness level across all simulation runs at all movement probabilities is presented below in figure 6.13.

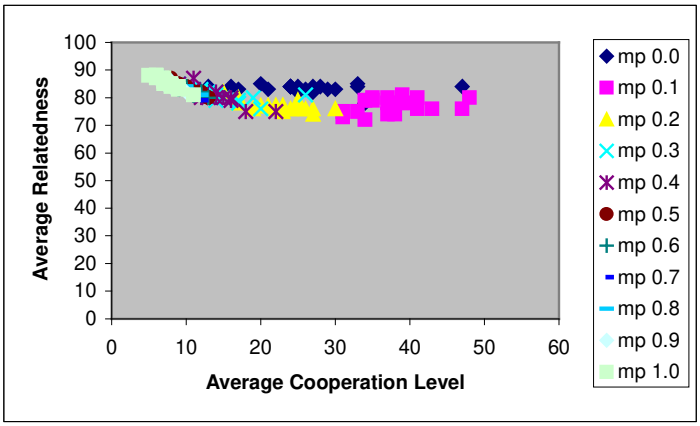

Figure 6.13. Scatter Plot of Average Cooperation Against Average Relatedness in the Pure Kin Selection Model at Movement Probabilities 0 to 1 with Interval 0.1

Table 6.6 below presents the correlation ***x´*** of average cooperation against average relatedness at each of the different movement probabilities studied.

Movement probability	**Correlation**
0	-0.179287
0.1	0.331309
0.2	-0.67705
0.3	-0.643188
0.4	-0.863647
0.5	-0.935613
0.6	-0.935638
0.7	-0.956721
0.8	-0.93079
0.9	-0.885445
1	-0.952188

Table 6.6. Correlation of Average Cooperation with Average Relatedness at Different Movement Probabilities in the Pure Kin Selection Model

As can be seen from table 6.6, there is a reasonable to very strong negative correlation at almost all the movement probabilities studied, apart from movement probabilities 0 and 0.1. A scatter plot of the correlation ***x´*** of average cooperation with average relatedness at one of these very strongly correlated movement probabilities is presented below in figure 6.14.

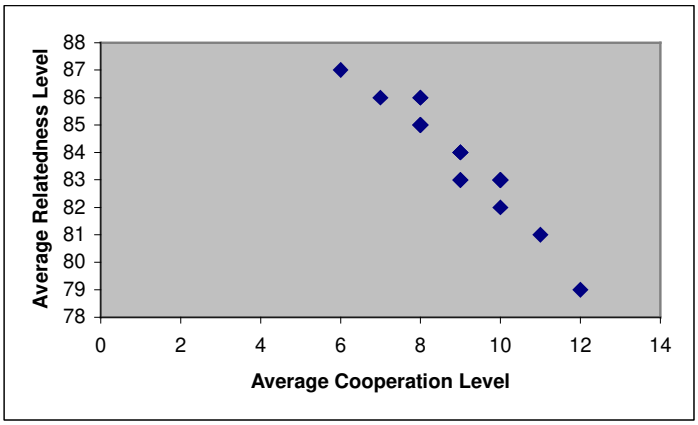

Figure 6.14. Scatter Plot of Average Cooperation Against Average Relatedness in the Pure Kin Selection Model at Movement Probability 0.7

6.4.6 Investigation of Results from the Pure Kin Selection Model with Local Population Regulation

The results from the pure kin selection model with local population regulation, presented in section 5.7.3, differ from the pure kin selection model in two ways. Firstly the average cooperation level is in general reduced in the model with local population regulation. Secondly, the average cooperation level does not fall at movement probability 0 as in the pure kin selection model, but instead continues to rise. This change in behaviour is the same as that observed in the Evolutionary Prisoner's Dilemma with local population regulation when compared to the standard Evolutionary Prisoner's Dilemma. The other effect of applying local population regulation to the Evolutionary Prisoner's Dilemma, identified in section 6.4.3, was to increase the correlation of average cooperation level, average relatedness level and average number of interactions. The same effect is not apparent when local population regulation is applied to the pure kin selection model, as the correlation x between average cooperation level and average relatedness level is reduced to 0.458977. However examining the correlation x' of cooperation and relatedness at each of the movement probabilities studied reveals more information, as shown below in table 6.7.

Movement probability	Correlation
0	0.321988
0.1	-0.597448
0.2	-0.844626
0.3	-0.826925
0.4	-0.717843
0.5	-0.748455
0.6	-0.76155
0.7	-0.77875
0.8	-0.434756
0.9	-0.746293
1	-0.897315

Table 6.7. Correlation of Average Cooperation with Average Relatedness at Different Movement Probabilities in the Pure Kin Selection Model with Local Population Regulation

As can be seen from table 6.7, there is a significant negative correlation between cooperation and relatedness at almost all of the movement probabilities studied, except for movement probability 0. This negative correlation, although slightly reduced, is very similar to that seen in the standard pure kin selection model as presented in section 6.4.5.

6.4.7 Comparison of Results from the Evolutionary Prisoner's Dilemma with Results from the Pure Reciprocal Cooperation Model

As section 6.4.4 compared cooperation in the Evolutionary Prisoner's Dilemma with cooperation in the pure kin selection model, the same is done in this section for the Evolutionary Prisoner's Dilemma and the pure reciprocal cooperation model. Comparing the average cooperation level in the Evolutionary Prisoner's Dilemma with the average cooperation level in the pure reciprocal cooperation model, shown in figures 5.5 and 5.24 respectively, does not show an obvious relationship. The degree of any relationship can be determined by calculating the correlation x'' of the average cooperation level at all movement probabilities in both models. Despite first appearances, the average cooperation levels in the two models are well correlated at 0.791345. The scatter plot of the average cooperation levels in the two models at all movement probabilities is presented below in figure 6.15.

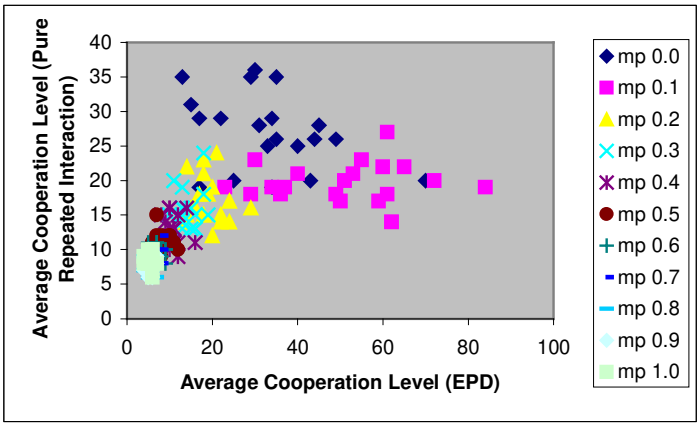

Figure 6.15. Scatter Plot of Average Cooperation in the EPD Against Average Cooperation in the Pure Reciprocal Cooperation Model at Movement Probabilities 0 to 1 with Interval 0.1

6.4.8 Investigation of Results from the Pure Reciprocal Cooperation Model

Examining the results from the pure reciprocal cooperation model, presented in section 5.6.2, shows some similarity in the behaviour of the average cooperation level and average number of interactions under varying movement probability, as shown in figures 5.24 and 5.26 respectively. Figure 6.16 below presents a scatter plot of the cooperation and number of interaction pairs from all the simulation runs at each movement probability studied. The correlation ***x*** of these values is high, at 0.926316.

It is gratifying to see that the average relatedness level, presented in figure 5.25, does not vary substantially with movement probability. This can be seen in the low correlation of average relatedness with movement probability, which at 0.160227 is substantially less than the correlation with relatedness in either the Evolutionary Prisoner's Dilemma or pure kin selection model, at –0.62569 and 0.619411 respectively. This low correlation between movement probability and relatedness indicates that the mechanism chosen to prevent relatedness of interactants from increasing under low movement probabilities, namely a global mating pool and random distribution of offspring within the entire environment, has been largely successful.

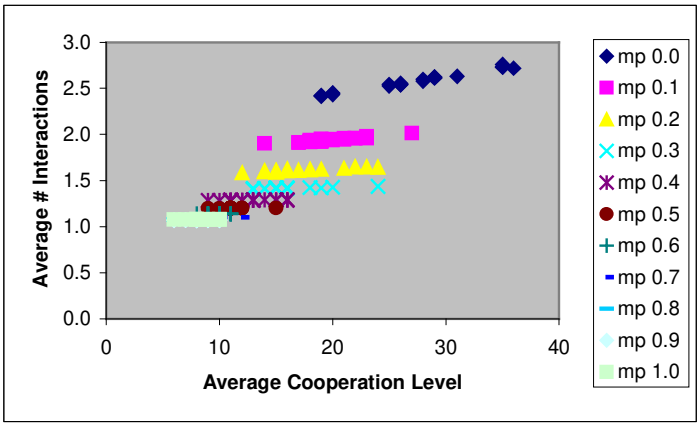

Figure 6.16. Scatter Plot of Average Cooperation Against Average Number of Interactions in the Pure Reciprocal Cooperation Model at Movement Probabilities 0 to 1 with Interval 0.1

Table 6.8 below presents the correlation x' of average cooperation level with average number of interactions calculated separately for each of the movement probabilities considered.

Movement probability	Correlation
0	0.992392
0.1	0.951749
0.2	0.949012
0.3	0.924097
0.4	0.713622
0.5	0.36404
0.6	0.014472
0.7	0.18775
0.8	0.491637
0.9	0.267746
1	0.170548

Table 6.8. Correlation of Average Cooperation with Average Number of Interactions at Different Movement Probabilities in the Pure Reciprocal Cooperation Model

As can be seen from table 6.8, there is a very high degree of correlation between the average cooperation level and the average number of interactions at low movement probabilities. This correlation is not in evidence for movement probabilities 0.5 to 1. Figure 6.17 below presents the scatter plot of average cooperation level against average number of interactions for movement probability 0.1, which is one of the movement probabilities at which these values exhibit a very high degree of correlation.

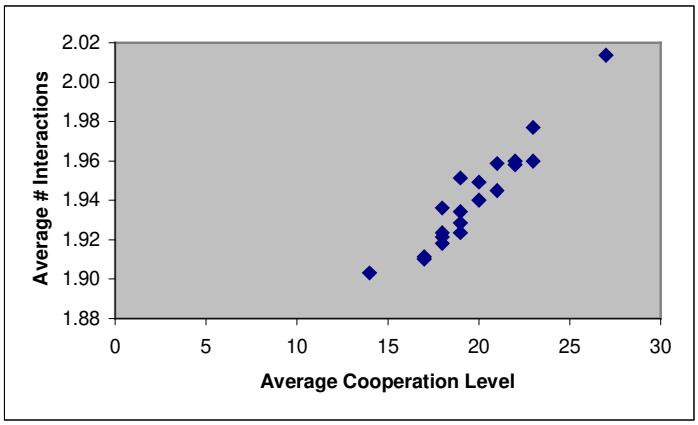

Figure 6.17. Scatter Plot of Average Cooperation Against Average Number of Interactions in the Pure Reciprocal Cooperation Model at Movement Probability 0.1

6.4.9 Discussion of Visualisations

In attempting to ascribe cooperation in the Evolutionary Prisoner's Dilemma to either kin selection or repeated interaction, additional evidence is available in the form of the population visualisations presented in section 5.11. These visualisations show the average cooperation level and average relatedness level within each local area of interaction for the entire environment. If kin selection operates in a model, then highly related and cooperative local populations should be present. However, the cooperation level in local populations subject to kin selection for altruism need not necessarily be 100%, as a kin-selected altruistic act involves one agent cooperating while the other defects, leading to an average cooperation level of 50%. Additionally the tension present in kin selection for altruism in the Prisoner's Dilemma and other 2 x 2 games, identified in section 6.2.3, may act against cooperative alleles becoming too frequent at the altruistic loci, in which case the cooperation level would again be below 100%. Given these considerations it should be possible to observe cells with a high degree of relatedness and a moderate to high degree of cooperation if kin selection is favouring altruism. Consulting table 4.1, such cells are coloured white in the visualisation for highly related highly cooperative cells, tending towards cyan in highly related cells with a lower cooperation level. An examination of the population visualisations for the Evolutionary Prisoner's Dilemma and pure kin selection model at movement probability 0.01, presented in figures 5.56 and 5.60 respectively, does reveal such cells in both models. The transition to this population state as movement probability falls can be seen in figures 5.53 to 5.55 for the Evolutionary Prisoner's Dilemma, and in figures 5.57 to 5.59 for the pure kin selection model. The Evolutionary Prisoner's Dilemma demonstrates both highly related highly cooperative cells, and some comparatively unrelated highly cooperative cells, represented by magenta in the visualisation. In contrast the pure kin selection model contains highly related highly cooperative cells, but also contains some uncooperative highly related cells, represented by cyan in the visualisation. The presence of highly cooperative unrelated cells in the Evolutionary Prisoner's Dilemma visualisation suggests that reciprocal cooperation may be operating in the model. Such cells can be observed because relatedness between interacting individuals is measured on the loci subject to kin selection for altruism and, as discussed in

section 3.3.2, mutual cooperation can become established between individuals that are completely unrelated at these loci. The presence of uncooperative highly related cells in the pure kin selection model visualisation supports the predictions of a force acting against kin selection made in section 6.2.3

In the Evolutionary Prisoner's Dilemma and pure kin selection model, the visualisation method has proved its usefulness by allowing differentiation between spatial zones with differing levels of cooperation and relatedness. Such local variations would not be detected by considering population averages alone. The visualisation method also motivated the investigation into population clustering in the Evolutionary Prisoner's Dilemma, described in section 6.3.3, by showing the population concentrating in some areas of the environment while leaving other areas empty, rather than spreading evenly throughout the entire environment.

In contrast to the Evolutionary Prisoner's Dilemma and pure kin selection model, the visualisations of the pure reciprocal cooperation model presented in figures 5.61 to 5.64 reveal little information. The only obvious change in the population as movement probability decreases is the disappearance of the highly cooperative unrelated cells and their replacement by uncooperative related cells and uncooperative unrelated cells, as noted in section 5.11.3.

6.4.10 Discussion of Results from the Evolutionary Prisoner's Dilemma, Pure Kin Selection and Pure Reciprocal Cooperation Models

The first thing to note of the results from the Evolutionary Prisoner's Dilemma, and the pure kin selection and pure reciprocal cooperation models, is that all the models exhibited an increase in cooperation as population viscosity increased, in agreement with the predictions of Hamilton (1964a) and Trivers (1971). In investigating the relative contributions of kin selection and repeated interaction to the cooperation observed in the Evolutionary Prisoner's Dilemma, the previous sections have compared results for average cooperation level, average relatedness level and average number of interactions from the Evolutionary Prisoner's Dilemma, pure kin selection and pure reciprocal cooperation models. This section discusses what these comparisons reveal.

In considering the results from the Evolutionary Prisoner's Dilemma, section 6.4.2 determined that the correlations between average cooperation level and either average relatedness or average number of interactions did not appear to be particularly significant. However a closer investigation of the relationship between average cooperation level and average number of interactions did reveal a very significant positive correlation at movement probabilities 0.1 to 0.4. This correlation suggests that repeated interaction is making a significant contribution to the amount of cooperation observed in the Evolutionary Prisoner's Dilemma at low movement probabilities. This could be because repeated interaction supports reciprocal cooperation, but repeated interaction is also required for kin-selected altruism to occur in the Prisoner's Dilemma, as identified previously in section 3.3.2. A comparison of the cooperation level in the Evolutionary Prisoner's Dilemma and in the pure kin selection model, presented in section 6.4.4, shows a very significant positive correlation between the two, whereas a

comparison of the cooperation levels in the Evolutionary Prisoner's Dilemma and pure reciprocal cooperation model shows a lower correlation. This may indicate that the cooperation observed in the Evolutionary Prisoner's Dilemma has similar causes to that observed in the pure kin selection model.

The population visualisations of the Evolutionary Prisoner's Dilemma and the pure kin selection model, discussed in the previous section, provide evidence in the form of highly related highly cooperative local populations that kin selection is operating in both models. However there is also evidence of cooperation through repeated interaction in the Evolutionary Prisoner's Dilemma, in the form of unrelated yet cooperative local populations. The evidence from the population visualisations supports the evidence from the other investigations into cooperation in the Evolutionary Prisoner's Dilemma presented in this chapter.

In the Evolutionary Prisoner's Dilemma with local population regulation, investigated in section 6.4.3, there is a significant correlation between average cooperation level and both average relatedness level and average number of interactions. However at individual movement probabilities, and in particular low movement probabilities, average cooperation is only correlated with average number of interactions. This suggests that in the Evolutionary Prisoner's Dilemma with local population regulation, as in the standard Evolutionary Prisoner's Dilemma, repeated interaction is making a significant contribution to observed cooperation at low movement probabilities. Once again, however, this observation is tempered by the knowledge that kin-selected altruism requires repeated interaction in the Evolutionary Prisoner's Dilemma.

The result of the investigation into the pure kin selection model, presented in section 6.4.5, is surprising. This investigation reveals that there is a reasonably strong negative correlation between average cooperation level and average relatedness level. This was the opposite of what was expected. The negative correlation arises because average cooperation increases under decreasing movement probability, whereas average relatedness decreases under decreasing movement probability. It was expected, as suggested by Hamilton (1964a), that increasing population viscosity by decreasing movement probability would increase the relatedness between interacting individuals, and hence lead to an increase in cooperation through the operation of kin selection. In fact this does occur in the Evolutionary Prisoner's Dilemma. The same decrease in relatedness under decreasing movement probability can be seen in the pure kin selection model with local population regulation, presented in section 5.7.3. That relatedness decreases as movement probability decreases, and is negatively correlated with the average cooperation level, is unexplained. However the explanation of the tension inherent in kin selection for altruism in the Prisoner's Dilemma and other 2 x 2 games, presented in section 6.2.3, may go some way to providing an answer to this problem.

In contrast the pure reciprocal cooperation model, investigated in section 6.4.8, behaved as expected, with average cooperation and average number of interactions increasing as movement probability decreases. The correlation of average cooperation level and average number of interactions is very significant, and also in the studies of individual movement probabilities average cooperation level and

average number of interactions are very significantly correlated, particularly at low movement probabilities.

6.4.11 A Note on the Difficulty of Separating Kin Selection and Reciprocal Cooperation in the Prisoner's Dilemma

Kin selection and reciprocal cooperation are closely related in the model studied, which uses the 2 x 2 games as its metaphor of social interaction. The Prisoner's Dilemma has been chosen as the best of the 2 x 2 games for studying kin selection and reciprocal cooperation in conjunction, yet the Prisoner's Dilemma is still subject to limitations in this respect. As noted in section 3.3.2, kin selected altruism can only occur in the Prisoner's Dilemma under certain conditions, and requires iterated interaction when acting on strategies for repeated interaction, making it difficult to distinguish between the operation of these two mechanisms in practice. This suggests that an alternative interaction model may better serve to study the relative contributions of kin selection and repeated interaction to cooperation. Additionally, section 3.5.1 has shown that kin selection can operate on strategies for reciprocal cooperation in the Prisoner's Dilemma, complicating the study of models intended only to study reciprocal cooperation. The difficulties associated with uncoupling kin selection and reciprocal cooperation in the Prisoner's Dilemma have implications for previous and further uses of it in studying these mechanisms, both separately as in Axelrod (1987) and Oliphant (1994), and in conjunction as in this thesis.

6.4.12 The Interaction of Kin Selection and Reciprocal Cooperation in the Prisoner's Dilemma

As discussed in section 2.3.1, Axelrod (1984) identified that one of the important properties of successful strategies for the iterated Prisoner's Dilemma, such as Tit-for-Tat, was being retaliatory. A retaliatory strategy immediately reciprocates a defection by its opponent, in order to discourage future attempts at exploitation. In a two-dimensional strategy chromosome for the Prisoner's Dilemma, one of the loci controlling the action taken after an opponent defects is the forgiving / vengeful locus. This locus was identified in section 3.3.2 as one of the loci subject to kin selection for altruism in the Prisoner's Dilemma. This raises an interesting potential conflict in the selection pressures on this locus. Selection for reciprocal cooperation should favour a defection allele for this locus, if Axelrod's assessment of the benefits of being retaliatory is correct. At the same time, kin selection should favour a cooperation allele at this locus if the conditions identified in section 6.2.2 are satisfied. Therefore, in the Prisoner's Dilemma, kin selection may act against the evolution of effective strategies for reciprocal cooperation. This is very interesting given Axelrod & Hamilton's (1981) suggestion that kin-selection for altruism could lead to the evolution of reciprocal cooperation. While the potential for a reduced demand for reciprocity among kin (Trivers, 1971) or conversely an increased demand for reciprocity among non-kin (Axelrod & Hamilton, 1981) has been briefly mentioned, this is the first explicit demonstration of how kin selection may inhibit the evolution of reciprocation.

6.5 Discussion of Other Results

This section discusses some of the other miscellaneous results which are not directly related to the central investigation into the contribution of kin selection and repeated interaction to observed cooperation, but that are nevertheless interesting.

6.5.1 Effects of Local Population Regulation

Section 5.7 presented results from applying local population regulation to the Evolutionary Prisoner's Dilemma and pure kin selection model. Local population regulation was discussed in section 1.4.3 as a potential force opposing kin selection in viscous populations. The motivation for studying local population regulation in the Evolutionary Prisoner's Dilemma and pure kin selection model was, therefore, to examine the effects it had on the results from these models. The average cooperation level in both these models is reduced by the introduction of local population regulation, in agreement with West Eberhard (1975), Grafen (1984) and Boyd (1982). However the observation that the cooperation level in the Evolutionary Prisoner's Dilemma with local population regulation is, at least at the lower movement probabilities, slightly higher than that observed in the pure reciprocal cooperation model presented in section 5.6.2, may indicate that fitness in the model has not been reduced completely to individual fitness as suggested by Wilson et al (1992). In considering the operation of local population regulation in the models, it should be noted that density regulation occurs before dispersal of offspring, whereas Taylor (1992a, 1992b) and Kelly (1994) have suggested that kin selection could be protected from local density regulation if density regulation occurred after dispersal.

While average cooperation level in the models was reduced by the introduction of local population regulation, in fact this reduction only occurred at movement probabilities above 0. At movement probability 0 the behaviour of both the Evolutionary Prisoner's Dilemma and the pure kin selection model was changed qualitatively by local population regulation. Whereas in both the Evolutionary Prisoner's Dilemma and the pure kin selection model there is a sharp discontinuity in average cooperation level between movement probabilities 0.1 and 0, in the corresponding models with local population regulation the cooperation level continues to increase from movement probabilities 0.1 to 0. It seems likely that this change in behaviour is brought about by the different maximum local population size at movement probability 0 under global and local population regulation. At movement probability 0, new subpopulations cannot become established, as agents are immobile. As some subpopulations become extinct, under global population regulation the remaining subpopulations can increase in size, until eventually there is only one subpopulation that has grown to the maximum population size permitted, and the model is effectively a panmictic, or freely mixing one. In contrast, under local population regulation, subpopulations are limited by the maximum local population size, which is 5 in the models studied. This accounts for the extinction of some populations before the simulation terminates, as seen in figures 5.35 and 5.39, because the subpopulations cannot grow large enough to guarantee their stability. In the models that do run to completion however, the expected average number of interactions between agents at movement probability 0 is much higher with local population regulation

than without, due to the reduced size of the subpopulations. This can be seen by considering the formula for the probability of two consecutive interactions between agents

$$u = \frac{(1-d)^2}{\overline{p}-1}\left((1-m)^2 + \frac{m^2}{8}\right)$$

from section 6.3.2. At $\boldsymbol{m} = 0$ the second term evaluates to 1. Holding this term constant, it is obvious that as the average local population size $\overline{p}$ decreases the probability of continued interaction $\boldsymbol{u}$ increases. With this increased shadow of the future, cooperation will be favoured.

6.5.2 Cognitive Requirements for the Iterated Prisoner's Dilemma

Oliphant (1994) has advised caution in choosing to investigate the iterated Prisoner's Dilemma, citing the requirement for increased cognitive capabilities in the players compared to the single-shot Prisoner's Dilemma, in order to recognise opponents and remember the history of interactions with them. Axelrod (1984) agreed, saying "*lower organisms must rely on mechanisms that drastically limit the number of different individuals[...] with which they can interact effectively*" and similarly "*reciprocal cooperation can be stable with the aid of a mechanism that reduces the amount of discrimination necessary*". This section therefore describes the results on the average number of opponents collected from the Evolutionary Prisoner's Dilemma and pure reciprocal cooperation model, and briefly discusses their implications.

The average number of opponents is presented for; the Evolutionary Prisoner's Dilemma without selection, the Evolutionary Prisoner's Dilemma, the pure reciprocal cooperation model, the pure reciprocal cooperation model with long agent lifespan, the Evolutionary Prisoner's Dilemma with local population regulation, the Evolutionary Prisoner's Dilemma with defector-disadvantageous payoffs, and the one-dimensional Evolutionary Prisoner's Dilemma, in figures 5.4, 5.9, 5.27, 5.31, 5.36, 5.43 and 5.47 respectively. In the Evolutionary Prisoner's Dilemma the average number of lifetime opponents remains around 2 until it reaches 3 to 4 at very low movement probabilities, while in the pure reciprocal cooperation model the average number of lifetime opponents starts around 2 then falls to 1 as movement probability approaches 0. In the Evolutionary Prisoner's Dilemma with local population regulation, the average number of lifetime opponents remains fairly constantly around 2. In the pure reciprocal cooperation model with long agent lifespan, the average number of lifetime opponents is significantly higher, starting at 6 at movement probability 1 but still falling to 1 at movement probability 0. In the Evolutionary Prisoner's Dilemma with defector-disadvantageous payoffs, the average number of lifetime opponents varies between 2 and 3, except for an abnormally high level of 7 at movement probability 0, while in the one-dimensional Evolutionary Prisoner's Dilemma the average number of lifetime opponents remains at around 3, only reaching 4 at movement probability 0. The Evolutionary Prisoner's Dilemma without selection provides the consistently highest average number of lifetime opponents, falling from 6 at movement probability 1 to 3 at movement probability 0.1, before rising to 8 at movement probability 0.

No conclusions are drawn on these results here. It is left to others to consider how the cognitive requirements for recognising a certain number of opponents as discussed above, and remembering the interaction history with each one sufficient to implement a two-dimensional strategy, affects the applicability of the results presented in this thesis to natural populations.

6.5.3 Results from the Battle of the Sexes

Section 5.10 presented results from the Evolutionary Prisoner's Dilemma with payoffs from the Battle of the Sexes, which was initially suggested in section 3.3. The results from using the Battle of the Sexes payoffs are not especially interesting, as can be seen from figure 5.50, which shows the average cooperation level in the model varying little and staying consistently under the mean cooperation level. Calculating the correlations x of the average cooperation level, average relatedness level and average number of interactions with each other gives the results presented in table 6.9 below.

Data	Correlation
Average cooperation / average relatedness	0.587367
Average cooperation / average number of interactions	0.993343
Average relatedness / average number of interactions	0.616515

Table 6.9. Correlation of Results in the Evolutionary Prisoner's Dilemma with Battle of the Sexes Payoffs

As can be seen from table 6.9, average cooperation is very well correlated with average number of interactions, but not particularly well correlated with average relatedness. It is not practical to calculate the correlations x' for average cooperation with average relatedness or average number of interactions at each of the movement probabilities studied. This is because the standard deviation of the average cooperation level is 0 at some of the movement probabilities studied, which leads to a division by zero in the calculation of the correlation. That the payoffs from the Battle of the Sexes have been designed to require agents to swap roles in order to achieve an average payoff equal to the environmental living cost, as described in section 5.10.1, may help explain the very high correlation between average cooperation and average number of interactions.

The results from the Battle of the Sexes are no more interesting than those from the Prisoner's Dilemma. While further study of the Battle of the Sexes is possible, it has not been undertaken in this thesis, as using the Battle of the Sexes gains little but adds unnecessary complexity. The Battle of the Sexes is inferior to the Prisoner's Dilemma as a means of studying both reciprocal cooperation and kin selection. As noted in section 6.2.1, kin-selected altruism cannot occur in the Battle of the Sexes as there is no cost for altruism. Apart from this, the main issue is the problem of defining cooperation in the Battle of the Sexes. As described in section 5.10.1, cooperation in the Battle of the Sexes can be defined as the percentage of interactions which result in coordination on either the AB or BA payoff. However this cooperation metric would result in a cooperation level of 100% for the situation where a pair of interacting agents repeatedly coordinate on the same payoff, with one agent consistently receiving the larger payoff. This could be considered as altruistic cooperation, however in order to measure reciprocal

cooperation in the Battle of the Sexes, a more complicated measure of cooperation must be used. In such a measure cooperative actions are those in which agents exchange roles at subsequent interactions, thereby sharing the payoffs fairly. The problem with this approach is that it requires the average number of interactions in the model to be sufficiently high, and as discussed in section 6.3.3, this is difficult to achieve in models based on the Evolutionary Prisoner's Dilemma. A related problem is that reciprocal cooperation requires the presence of at least two types of agents, those that play A followed by B and those that play B followed by A, and reciprocal cooperation will only occur when these two different types of agent interact. The Prisoner's Dilemma is not subject to these problems, as it allows reciprocal cooperation to occur in a single interaction in the form of mutual cooperation, and agents with strategies such as Tit-for-Tat can achieve reciprocal cooperation with agents using an identical strategy.

In summary, the use of the Battle of the Sexes in a model studying cooperation through repeated interaction introduces unnecessary complexity that is not present in the Prisoner's Dilemma, while the study of cooperation through kin selection using the Battle of the Sexes is limited by the fact that it does not support kin-selected altruism, unlike the Prisoner's Dilemma.

6.5.4 Results from the One-Dimensional Evolutionary Prisoner's Dilemma

The results from the one-dimensional Evolutionary Prisoner's Dilemma, presented in section 5.8.2, show interesting behaviour in the variation of average number of interactions with movement probability, presented in figure 5.46. The curve of average number of interactions under varying movement probability displays good rotational symmetry, so if the curve is rotated by 180 degrees it is still a very good match against the unrotated curve. The reason behind, and significance of, this symmetry is unknown, and could prove an interesting research problem for further investigation.

6.6 A Note on the Behaviour of the Models with No Mobility

The behaviour of the models studied is qualitatively different when movement probability is 0 to when it is higher. An indication of this can be seen in many of the results presented in chapter 5. For example the results for average cooperation level and average number of interactions in the Evolutionary Prisoner's Dilemma, presented in section 5.4.2, show marked discontinuities between movement probabilities 0.1 and 0. This qualitative difference occurs because, at movement probability 0, the population is the most viscous it can be, with no agent mobility at all. This population state gives rise to a peculiar set of circumstances in which the global population is either divided into several fully-mixing subpopulations, or comprises a single fully-mixing population. In either case new subpopulations cannot be formed, existing subpopulations can only become extinct. Additionally, agents cannot migrate between subpopulations. This population structure therefore closely resembles that required for the theory of group selection by selective extinction of groups (Maynard Smith, 1976) except that the groups concerned are completely, rather than partially, reproductively isolated, and the groups cannot reproduce. Given that the groups cannot reproduce, the inevitable consequence of repeated extinction of groups is

complete extinction of the population. As noted in section 6.5.1, as groups become extinct under global population regulation the remaining groups can increase in size, while under local population regulation the remaining groups cannot grow, and this can have implications for the stability of populations under the different regulation schemes with smaller groups likely to be less stable.

6.7 Conclusion

This chapter has investigated the extent to which the models studied, in particular the Evolutionary Prisoner's Dilemma, support the operation of kin selection for altruism and reciprocal cooperation. Of particular interest is the identification of the conflict inherent in kin selection for altruism in the Prisoner's Dilemma and other 2 x 2 games, which is described in section 6.2.3. This conflict is likely to have been effective in the Evolutionary Prisoner's Dilemma, and has implications for the choice of interaction model in studies into kin selection and reciprocal cooperation that are discussed in the next chapter. This chapter has also discussed the mathematical model of expected interaction length from Marshall & Rowe (2000) and, although it has limitations, has used it to demonstrate that the Evolutionary Prisoner's Dilemma is unlikely to provide conditions that fully support reciprocal cooperation as defined by Axelrod's (1984) condition for the collective stability of Tit-for-Tat. This result has been generalised to all viscous populations in which local population density increases with population viscosity, such as the Evolutionary Prisoner's Dilemma. In such populations, the question of how much support is provided for reciprocal cooperation rests on the relative rates of increase of the average local population size, and of the maximum local population required for the collective stability of Tit-for-Tat, as movement probability decreases. In light of this result, a variant on the Evolutionary Prisoner's Dilemma with extended interaction length has also been studied and shown to provide much better support for reciprocal cooperation, with a corresponding increase in cooperation levels.

Additional results have been presented in this chapter relating to the effects of local population regulation on kin selection, the cognitive requirements for the iterated Prisoner's Dilemma, and the effect of modifying the payoffs and dimensionality of the environment in the Evolutionary Prisoner's Dilemma. The Battle of the Sexes has also been considered as an alternative interaction model to the Prisoner's Dilemma for the study of kin-selected altruism and reciprocal cooperation, and has been shown to introduce unnecessary complication into the study of reciprocal cooperation when compared to the Prisoner's Dilemma, while not supporting kin-selected altruism at all.

As for the question of whether cooperation observed in the Evolutionary Prisoner's Dilemma is attributable to kin selection or repeated interaction, evidence is available supporting both. Cooperation in the Evolutionary Prisoner's Dilemma appears to be better correlated with number of interactions than with relatedness, especially at low movement probabilities, which is suggestive of the significance of repeated interaction. However, as identified in section 3.3.2, kin-selected altruism in the Evolutionary Prisoner's Dilemma requires repeated interaction in order to occur, therefore a high degree of correlation between number of interactions and cooperation level does not necessarily indicate that reciprocal cooperation is at work. Furthermore, cooperation in the Evolutionary Prisoner's Dilemma is better

correlated with cooperation in the pure kin selection model than with cooperation in the pure reciprocal cooperation model. Finally, the population visualisations of the Evolutionary Prisoner's Dilemma model at very low movement probability show local population behaviour consistent with the operation of both kin selection and reciprocal cooperation. Although evidence exists for the operation of both kin selection and reciprocal cooperation in the Evolutionary Prisoner's Dilemma, the detailed analysis presented here has revealed that determining their relative contributions is more complicated than previously anticipated, partly due to the way in which kin-selected altruism is dependent on repeated interaction in this model.

The main contribution of this chapter, however, is the identification of a possible conflict in the selective forces acting on kin-selected altruism and reciprocal cooperation in the Prisoner's Dilemma. As discussed in section 6.4.12, kin selection for altruism may act against the evolution of strategies that reciprocate defection, which were argued by Axelrod (1984) to be significant in the evolution of reciprocal cooperation. This fact is particularly interesting given Axelrod & Hamilton's (1981) suggestion that kin-selected altruism could be a first step towards the evolution of reciprocal cooperation.

Chapter 7 – Conclusions and Further Work

7.1 Introduction

This chapter concludes the thesis and is arranged as follows. In section 7.2 the research presented is summarised, and in section 7.3 the research methodology used is evaluated. Section 7.4 summarises the contributions of the research presented. Further work arising from this research is identified and discussed in section 7.5 while finally, in section 7.6, conclusions are drawn on the successes and failures of the research.

7.2 Summary of the Research

This thesis has presented an investigation into the evolution of cooperative behaviour in populations of selfish individuals. The mechanisms considered as explanations for such cooperation are kin selection, as proposed by Hamilton (1964a, 1964b), and reciprocal cooperation, as proposed by Trivers (1971). While these mechanisms have been studied separately, they have not been studied in conjunction, despite proposals such as Axelrod & Hamilton's (1981) that kin-selected altruism could be a first step towards the evolution of reciprocal cooperation. Trivers (1971) also provided motivation for the study of kin selection and reciprocal cooperation together, by noting that the two mechanisms are favoured by the same conditions, leading to difficulties in discriminating between their operation, and by arguing that the two mechanisms can occur in parallel and interact with each other. Both of these mechanisms were predicted to be supported by viscous populations (Hamilton, 1964a; Trivers, 1971), which are spatially distributed populations in which the mobility of members of the population is limited, and interactions and mating between members of the population take place locally. This motivated the design of a viscous population agent-based simulation model to study these predictions. In the course of choosing an interaction model suitable for supporting kin-selected altruism and reciprocal cooperation, the class of non-cooperative 2 x 2 games were considered and the Prisoner's Dilemma and the Battle of the Sexes identified as the two most suitable games.

The use of the Prisoner's Dilemma in previous studies into both kin selection and reciprocal cooperation was evaluated, and in doing so the exact requirements for kin selection to be able to favour altruism in the Prisoner's Dilemma and other 2 x 2 games were identified, as well as the potential for inadvertently supporting altruism through kin selection in models designed solely to investigate reciprocal cooperation. Using this knowledge, this thesis presented the designs of models supporting both kin selection for altruism and reciprocal cooperation, kin selection for altruism only, and reciprocal cooperation only. These models were implemented using genetic algorithms operating on two-dimensional strategies for the class of 2 x 2 games. Results have been presented from all these models that agree with the predictions of Hamilton (1964a) and Trivers (1971) for increased cooperation in viscous populations.

In an attempt to determine the relative contributions of kin selection and reciprocal cooperation to observed cooperation, this thesis developed several tools, including a spatial visualisation tool for observing the level of cooperation and relatedness in local populations, and mathematical tools for determining the extent to which both kin-selected altruism and reciprocal cooperation are supported by any parameter configuration of the models. In the course of the development of these mathematical tools, a conflict inherent in the operation of kin selection for altruism in the Prisoner's Dilemma and other 2 x 2 games has been identified. At the same time, a complicating factor in the support for reciprocal cooperation in a certain class of viscous populations has been identified. The interactions and dependencies between kin selection for altruism and reciprocal cooperation have also been explored, and a potential conflict between the operation of these two mechanisms in the Prisoner's Dilemma has been identified, as well as the dependency of kin-selection for altruism on repeated interaction in the models studied.

In addition to the main results from the models described above, results have been presented from preliminary investigations into the effects of local population regulation on the operation of kin selection, the use of the Battle of the Sexes as an interaction model supporting kin selection and reciprocal cooperation, and changes in the magnitude of interaction payoffs and the dimensionality of the standard model. The results of the investigation into the Battle of the Sexes have highlighted its inferiority to the Prisoner's Dilemma as an interaction method that supports both kin-selected altruism and reciprocal cooperation. The results of the investigation into the relative contribution of kin selection for altruism and repeated interaction to observed cooperation show that both mechanisms are at work, but are unable to determine the degree of their contributions, due to the interactions and dependencies between these mechanisms that have been revealed in this thesis.

7.3 Review of the Research Methodology

In section 1.2, Di Paolo et al's (2000) concept of an "opaque thought experiment" was chosen as the approach to be used in investigating the model presented. Briefly, the idea of the "opaque thought experiment" is that a computer simulation is a kind of thought experiment that uses "*the relationships between patterns in the simulation to explore the relationships between theoretical terms corresponding to analogous natural patterns*." So, the experiment is designed as a theoretical tool to understand and possibly revise the relationship between theoretical terms. Yet at the same time the experiment is sufficiently complex that it displays "explanatory opacity", meaning that the experiment must be systematically explored before it can be understood, and that this understanding can feed back into the underlying theory. Di Paolo et al identified three phases in their experimental process, which are reproduced below:

1. *Exploratory phase:* After the initial simulation model is built, explore different cases of interest, define relevant observables, record patterns, re-define observables or alter model if necessary.
2. *Experimental phase:* Formulate hypotheses that organise observations, undertake crucial "experiments" to test these hypotheses, explain what goes on in the simulation in these terms.

3. *Explanatory phase:* Relate the organisation of observations to the *theories* about natural phenomena and the hypotheses that motivated the construction of the model in the first place, make explicit the theoretical consequences.

The experimental process used in this thesis does not strictly follow the three phases described above. Rather than undertake an exploratory phase and use the results from that to formulate hypotheses for testing in the experimental phase, this thesis has started out with an existing hypothesis and designed a model to test that hypothesis, namely that viscous populations favour both kin selection and reciprocal cooperation. The explanatory phase has revealed a behaviour of the model, namely population clustering, which has implications for the theory of reciprocal cooperation in viscous populations. This is a good example of "explanatory opacity" in the form of a behaviour not explicitly included in the initial design of the model being observed and feeding back into the underlying theory. Also the explanatory phase, while confirming the hypothesis tested, has made a contribution in the form of identifying inadequacies in the design of the model that could feed back into a redesign of that model, as well as details of the way in which the two mechanisms under investigation interact in the model, which may inform either the underlying theory or the redesign of the model. Perhaps then the research presented in this thesis is actually best considered as a single iteration of the process described above. A re-design of the model would begin a second iteration of that process.

In summary and given the above considerations, it seems that the methodology used in investigating the model is similar in spirit to that advocated by Di Paolo et al, if not in exact detail. This similarity lies in the use of an investigative approach to explain the results from the simulation model, and to try and understand the relationship of the different processes implemented in the model to each other.

7.4 Summary of Contributions

The main contributions of the research presented in this thesis are not the results presented from any specific model, but rather an improved understanding of the operation of kin selection for altruism and reciprocal cooperation in populations of self-interested individuals, the way they interact in the 2 x 2 games, and the conditions necessary to support these processes. In particular the research contributions presented in this thesis are:

- an evaluation of 2 x 2 games suitable for studying both kin-selected altruism and reciprocal cooperation. Of the non-cooperative 2 x 2 games, the Prisoner's Dilemma and the Battle of the Sexes are identified as supporting both kin selection and reciprocal cooperation, with the Prisoner's Dilemma additionally being capable of supporting kin-selected altruism. A comparison of these two games has revealed the Prisoner's Dilemma to be superior to the Battle of the Sexes for the study of both kin selection and reciprocal cooperation.
- a detailed investigation of the operation of kin selection on altruism in the Prisoner's Dilemma and other 2 x 2 games. Some previous studies have either weakly invoked kin selection where kin-selected altruism cannot occur, or failed to consider its operation in models designed to support only reciprocal cooperation.

- the identification of a conflict inherent in the operation of kin selection on altruism in the Prisoner's Dilemma and other 2 x 2 games. This conflict has not previously been recognised and has implications for the degree of support for kin-selected altruism provided by models based on 2 x 2 games such as the Prisoner's Dilemma.
- the identification of the dependency of kin-selected altruism in the Prisoner's Dilemma on repeated interaction. This dependency has implications for attempts to differentiate between cooperation due to kin selection and due to repeated interaction in the same model.
- the design and implementation of a model that supports the operation both of kin selection for altruism and reciprocal cooperation, and which provides conditions favourable to both in the form of a viscous population. The study of a model designed explicitly to support both kin selection for altruism and reciprocal cooperation has not been carried out before, yet is interesting as some (Axelrod & Hamilton, 1981) have proposed that kin-selected altruism could be a preliminary step in the evolution of reciprocal cooperation, while others (Trivers, 1971) have identified problems in differentiating between the operation of the two mechanisms, and proposed that they can occur in parallel and interact with each other.
- the development of mathematical tools to assess the degree to which such models support the operation of kin selection for altruism and reciprocal cooperation.
- the identification of a potential conflict in the operation of kin selection for altruism and reciprocal cooperation in the Prisoner's Dilemma, so that kin selection may hinder the evolution of strategies that retaliate to defection with defection.
- the identification that in viscous populations in which local population density increases with viscosity, the degree of support for reciprocal cooperation is dependent on the relative rates of increase, of the average local population size, and of the maximum local population size required for the stability of reciprocal cooperation, as movement probability decreases

7.5 Further Work

The results presented in chapter 5, and the discussions of them presented in chapter 6, ask as many new questions as they answer. Therefore it is easy to identify further work that can be undertaken on the ideas presented in this thesis.

7.5.1 Modification of the Models

Modification of the models allows new avenues of research to be explored. As noted in section 6.5.1 during the discussion of the effects of local population regulation on kin selection, population regulation occurs before dispersal of offspring in the model, whereas Taylor (1992a, 1992b) and Kelly (1994) have suggested that kin selection may be protected from local population regulation if dispersal occurs before such regulation. A simple modification of the order of execution of the Evolutionary Prisoner's Dilemma and the pure kin selection model would allow this claim to be investigated further and could contribute to the debate on the significance of local population regulation for kin selection.

Similarly, section 4.4.2 discusses the implementation of asynchronous update in the Evolutionary Prisoner's Dilemma and models derived from it. The implementation of an asynchronous update mechanism is a response to Huberman & Glance's (1993) criticisms of synchronous update in models, and their claim that synchronous update introduces artefacts into the results of such models. Experimentation with the implementation of asynchronous update in the Evolutionary Prisoner's Dilemma may yield interesting results which shed new light on Huberman & Glance's ideas and which have implications for a whole class of computer simulation models.

In fact, the Evolutionary Prisoner's Dilemma, like all complex systems, gives rise to complex macro-behaviour from comparatively simple micro-rules. There is much potential for experimental variation of these micro-rules to explore the effects of the assumptions and design decisions built into them.

7.5.2 Investigation of Unusual Results

This thesis has attempted explanations of some of the results it presents, such as the discussion in section 6.5.1 of the change in model behaviour at movement probability 0 when local population regulation is applied. However there are several other results for which explanations have not been attempted. Of these results, perhaps the most interesting is the unusual behaviour of the average number of interactions under varying movement probability in the one-dimensional Evolutionary Prisoner's Dilemma, presented in figure 5.46. As noted in section 5.8.2, the curve of the average number of interactions exhibits a remarkably high degree of rotational symmetry. Of course, the characteristic of displaying rotational symmetry is as much a property of the observer who ascribes that characteristic as of the system itself, so the observation that the average number of interactions curve does display rotational symmetry may be meaningless. However, it may also indicate some fundamental property of the model that merits investigation. Another significant result that merits further investigation is the decrease in relatedness level under decreasing movement probability in the pure kin selection model both with and without local population regulation. This decrease in relatedness under increasing population viscosity is the opposite of what Hamilton (1964a) predicted in viscous populations. Furthermore the same behaviour is not exhibited in the Evolutionary Prisoner's Dilemma, in which relatedness increases with population viscosity as predicted by Hamilton. Further investigation into the reasons for this phenomenon could prove valuable.

7.5.3 Exploration of Parameters

The number of parameters that can be subjected to variation in the Evolutionary Prisoner's Dilemma and related models is very large. Furthermore these parameters almost all have a potentially infinite range of acceptable values. This leads to an infinite number of different model configurations, of which only a handful have been studied in this thesis. Clearly there is great scope for exploration of different configurations of the models presented here. Such exploration has been attempted with the variations in such parameters as agent lifespan, magnitude of payoffs and dimensionality of the environment presented in this thesis. Systematic exploration of the available model configurations is a tedious and time-consuming process, and is not practical for such a large parameter space. However problems with highly dimensional sets of parameters, whose relationship with each other is not fully understood, provide an

excellent application for evolutionary algorithms. Bankes & Gillogly (1994) have already proposed the use of evolutionary programming for exploring the parameter spaces of computation models but a genetic algorithm could also be used. In order to use a genetic algorithm, all that need be determined is an appropriate genetic representation and set of genetic operators, and a fitness function for assessing the quality of solutions generated by the genetic algorithm. An example fitness function could attribute high fitness to model configurations that give rise to a high average level of cooperation with a small standard deviation, and low fitness to model configurations giving rise to low average levels of cooperation, high standard deviations, or both. Such a fitness function has the advantage of being easily automated. Evolution under the genetic algorithm would then be expected to give rise to increasingly cooperative models. Examination of these models may provide further insights into the factors that contribute to increased cooperation. This use of genetic algorithms as an optimisation tool contrasts with the use of genetic algorithms in the rest of this thesis, as a tool for studying co-adaptation.

7.5.4 Fitness Visualisation

Section 4.6.2 presented a method of visualising kin selection to complement the numerical results from the models, and aid in their interpretation. It may also prove useful to visualise the fitness landscape in the models. The fitness landscape arises from the fitness function, and is an n-dimensional space that specifies the fitness of an individual occupying any of the points it contains, where an individual's location in the space is specified by their genotype. The dimensionality of the fitness landscape is determined by genotype length, so for the Evolutionary Prisoner's Dilemma, which has a five-locus genotype, the fitness landscape is five-dimensional. The main problem in fitness landscaping then, is to compress a space with more than three dimensions into a three-dimensional representation. Approaches to this problem include Sammon mapping (Sammon, 1969), the "Search Space Matrix" technique (Collins, 1998) and the "Fitness Landscaping" algorithm (Anastasoff, 2000). As the Evolutionary Prisoner's Dilemma is a co-adaptive system the fitness function is defined by the state of the population itself, therefore the fitness landscape will change over time. It may also be interesting to visualise the location of the population on the fitness landscape, in order to observe the process of co-adaptation.

7.5.5 Alternative Interaction Models

This thesis took the non-cooperative 2 x 2 games as the starting point in the search for an interaction model that supports both kin-selected altruism and reciprocal cooperation. Of these games, the Prisoner's Dilemma and the Battle of the Sexes were identified as being most suitable.

During the course of the investigation, certain restrictions on the support for kin-selected altruism in the Prisoner's Dilemma have been identified. Problems in uncoupling kin selection and reciprocal cooperation in the Prisoner's Dilemma have been noted in section 6.4.11, such as the potential for kin selection for altruism to act on strategies for reciprocal cooperation. Furthermore, kin selected altruism can only occur in the Prisoner's Dilemma with two-dimensional strategies when the interactants chose opposite actions in their previous encounter, resulting in each individual using a different locus to determine their current action. The effect of this is that only a subset of the loci in the genotype for a two-dimensional strategy are subject to kin selection for altruism, and also that such selection can only occur

in populations where pairs of agents tend to interact more than once. Finally, this thesis has identified that there is a conflict between the operation of kin selection at each of these loci, so that the success of kin selection at one of these loci will hinder its operation at the other.

The Battle of the Sexes is also subject to problems as discussed in section 6.5.3. One problem is that kin-selected altruism cannot occur in the Battle of the Sexes as there is no cost for altruism. Another problem is that the definition of cooperation in the Battle of the Sexes is more complicated than in the Prisoner's Dilemma. Yet another problem is that reciprocal cooperation requires agents to alternate actions in order to equitably share the payoffs. This introduces the requirement that agent pairs typically interact for long enough to enable this kind of payoff sharing, and also the requirement for two different types of agent where reciprocal cooperation can only occur between agents of different types.

Given that there are certain weakness in both the Prisoner's Dilemma and the Battle of the Sexes as interaction models for studying kin-selected altruism and reciprocal cooperation in conjunction, the search for a different interaction model less subject to such limitations may prove fruitful.

7.6 Conclusion

The central hypothesis underlying this thesis, that viscous populations favour both kin selection for altruism and reciprocal cooperation, has been supported by the results presented herein. However the main aim of this thesis was to develop methods able to assess the relative contributions of kin selection and repeated interaction to observed cooperation in the models studied. Unfortunately the application of these methods to the models studied has revealed unanticipated complications, for attempts to distinguish between kin selection and reciprocal cooperation as explanations for observed cooperation, and for attempts to establish the relative magnitude of their contributions. This is in part due to the dependency of kin-selected altruism on repeated interaction in order to occur in the Prisoner's Dilemma. However this thesis has still contributed to the understanding of kin selection and reciprocal cooperation in viscous populations, as described below.

Firstly, as noted above, this thesis supports the predictions of Hamilton (1964a) and Trivers (1971) that viscous populations provide conditions for increased cooperation through kin selection and repeated interaction respectively. Secondly, this thesis has identified that in viscous populations in which increased viscosity leads to increased local population density, this increased density can act against the effects of viscosity that promote repeated interaction, thus reducing the degree of support for reciprocal cooperation. This clustering effect is particularly likely to be observed in populations that are subject to the Allee effect (Allee, 1931), in which individual members of the population are dependent on the presence in their vicinity of other individuals from the same population in order to survive. The Evolutionary Prisoner's Dilemma model provides an example of a population exhibiting the Allee effect, due to the requirement for individuals in the model to interact with others in order to obtain sufficient energy to cover their continuous energy expenditure. In such clustering viscous populations, cooperation may be rescued by increasing the duration of each separate encounter between individuals, as was done

in one of the experiments presented in this thesis, possibly through the introduction of social customs or laws regarding interaction (Axelrod, 1984).

Finally, this thesis has contributed an increase in the understanding of the mechanisms of kin-selected altruism and reciprocal cooperation. In particular the operation of kin selection in the Prisoner's Dilemma has been investigated thoroughly. One of the main contributions of this investigation is the understanding of the way in which kin selection for altruism and reciprocal cooperation interact and are dependent. In particular, it has been demonstrated how kin selection may act against the evolution of effective strategies for reciprocal cooperation, which is interesting in light of suggestions that kin-selected altruism could precede the evolution of reciprocal cooperation (Axelrod & Hamilton, 1981). This contribution vindicates the approach taken in this thesis of studying kin-selected altruism and reciprocal cooperation in conjunction, yet it is an open question as to whether this represents a contribution to the theory of the evolution of cooperation, or to the study of the evolution of cooperation. It is arguable that the contribution is of the former kind, as it does not take too much imagination to see how kin selection may inhibit behaviour that harms relatives, such as retaliation. However it is hoped that even if the contribution is of the latter kind, the insight it provides into how kin-selection and reciprocal cooperation operate within 2 x 2 games is a valuable one, which, given the widespread use of 2 x 2 games to study problems of cooperation, seems likely.

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Glossary of Biological Terms

Allele. A *gene* that can occupy a particular *locus*. One *locus* may have many *alleles*, or rival *genes* for that *locus*. For example the *locus* for controlling eye colour may have *alleles* for blue eyes and brown eyes, or the *locus* for controlling aggression may have *alleles* for aggressiveness or meekness.

Deme. A sub-population within which breeding occurs randomly.

Diploid. See *ploidy*.

Dominance. In the *diploid* system, a *dominant allele* is one that will lead to expression of the trait that it encodes if it is present at a *locus*, regardless of the other *allele* at that *locus*.

Epistasis. The situation occurring when the *allele* at one *locus* (the *epistatic gene*) overrides the *allele* at another *locus* (the *hypostatic gene*) so that the *epistatic gene* alone controls the *phenotype*.

Gamete. In the *diploid* system a *gamete* is the *haploid* reproductive *genotype* that combines with a *gamete* from the other parent to form a *zygote*.

Gene. The smallest unit of *selection*. A *gene* encodes for some characteristic to be expressed in the *phenotype*, such as blue eyes or aggressiveness.

Gene frequency. The proportions of different *alleles* of a *gene* at one *locus* in a population.

Gene pool. The sum total of all *genes* in the *genotypes* of all individuals in a *deme*, or the sum total of *genes* in *gametes* of a population (two copies per individual, which may or may not be the same *allele*).

Genotype. A collection of *genes* fully specifying an individual's genetic composition.

Haploid. See *ploidy*.

Haplo-diploid. See *ploidy*.

Hardy-Weinberg equilibrium. In the *diploid* system, the frequency of *homozygous dominant*, *heterozygous* and *homozygous recessive allele* combinations at a *locus* in the absence of *selection*.

Heterozygous. In the *diploid* system a *heterozygous locus* is one that contains two different *alleles*.

Homozygous. In the *diploid* system, a *homozygous locus* is one that contains two identical *alleles*.

Hypostasis. See *epistasis*.

Linkage equilibrium / disequilibrium. If more than one *locus* is involved in determining a trait, the *loci* can be connected (disequilibrium) or independent (equilibrium). Independence is defined as the *allele* frequencies at one *locus* having no effect on the *allele* frequencies at another *locus*.

Locus. A location on the *genotype* that controls the expression of a particular trait according to the *allele* at that location.

Meiosis. In the *diploid* system, the process by which *alleles* for each *locus* are chosen for inclusion in the *gamete*.

Mendelian ratio. The ratio of different offspring *phenotypes* expected in a *diploid* species when breeding *homozygous* parents with two distinct *phenotypes*.

Phenotype. The expression of an individual's *genotype*, possibly modified by environmental effects. The *phenotype* can be considered to correspond to the individual's physical body and its behaviour.

Ploidy. Different genetic systems exist according to the number of *alleles* that occupy one *locus*. The simplest genetic system is *haploid*, in which each *locus* contains only one *allele*. In the *diploid* system, each *locus* contains two *alleles*, and the trait controlled by that *locus* is determined by the combination of those two *alleles* according to their *dominance* or *recessiveness*. The *haplo-diploid* system occurs in various species of social insect, such as ants, and is characterised by males having *haploid genotypes* and females having *diploid genotypes*.

Quantitative genetics. The study of traits that result from a combination of the interaction of many *loci* and the environment.

Recessiveness. In the *diploid* system, a *recessive allele* is one that will lead to expression of the trait that it encodes only if the other *allele* at the *locus* in question is the same.

Selection. The evolutionary force acting on fitness differences due to a trait, resulting in differential reproduction of the individual expressing the trait.

Zygote. In the *diploid* system a *zygote* is the *diploid* offspring *genotype* resulting from the fusion of two *gametes*, one from each parent.

Glossary of Game Theoretical Terms

2 x 2 games. The class of games involving two players, each with a choice of two alternative actions.

Best reply. A strategy against which no other strategy can receive a higher payoff than the strategy does when played against itself.

Deficient equilibrium. An *equilibrium* such that there exists some other outcome of the game which results in higher payoffs for both players.

Equilibrium. An outcome of a game in which no player can improve their payoff by changing their chosen action, given the action chosen by the other player.

Evolutionary Stable Strategy. A strategy such that, if used by the majority of a population, there is no other strategy that receives a higher payoff in that population.

Maximin strategy. A strategy designed to minimise a player's loss in a game if such a loss should occur.

Minimax strategy. A *maximin strategy* in a *zero-sum game*.

Nash equilibrium. A strategy that is a *best reply* to itself.

Non-trivial game. A game in which players choosing the action that gives the best payoff regardless of the other's action do not achieve the largest available payoff.

Non zero-sum game. A game in which a gain for one player does not necessarily imply a loss for the other.

Pareto equilibrium. An *equilibrium* such that there is no other outcome of the game which results in higher payoffs for both players.

Symmetric game. A game in which the payoffs are the same from the point of view of both players.

Zero-sum game. A game in which a gain for one player implies a loss for the other.

Glossary of Symbols

This glossary presents the symbols used in this thesis, and their definitions where appropriate. The numbers in brackets refer to the section each symbol was first introduced in.

A_t The set of agents in the population that are alive at timestep t (5.2)

$\overline{A}$ The set of all agents that exist in the entire duration of the simulation (5.2)

b The fitness benefit to the recipient of an altruistic act (1.4.1)

c The fitness cost to the donor of an altruistic act (1.4.1)

$\bar{c}$ The average cooperation level (5.2.1)

$\overline{c_2}$ The average cooperation level in the Battle of the Sexes (5.10.1)

D The genetic diversity of a population (4.6.1)

d The environmental probability of death (4.4)

$\bar{e}$ The average number of lifetime opponents (5.2.6)

I_t The set of pairs of agents in the population that interact at timestep t (5.2)

$\overline{I}$ The set of all pairs of agents that interact in the entire duration of the simulation (5.2)

i The expected number of interactions (6.3.1) $i = 1 / (1 - w)$

i_c The inclusive fitness of a cooperation allele (6.2.2)

i_d The inclusive fitness of a defection allele (6.2.2)

m The agent movement probability (6.3.2)

P The Punishment payoff in the Prisoner's Dilemma (1.3.1)

p The proportion of the maximum population that the current population represents (4.4)

$\bar{p}$ The average cell population (5.2.5)

$\bar{p}'$ The required local population size for an expected number of interactions ν (6.3.3)

Q_t The set of populated cells at timestep t (5.2)

$\bar{Q}$ The set of all populated cells in the entire duration of the simulation (5.2)

R The Reward payoff in the Prisoner's Dilemma (1.3.1)

r The coefficient of relationship between the donor and recipient of an altruistic act (1.4.1)

r' The relatedness threshold for altruism to be favoured by kin selection (6.2.2)

$\bar{r}$ The average relatedness level (5.2.2)

$\bar{r}_1$ The average relatedness calculated on the entire genotype (5.2.2)

$\bar{r}_2$ The average relatedness calculated only on the loci subject to kin selection (5.2.2)

S The Suckers Payoff in the Prisoner's Dilemma (1.3.1)

T The Temptation payoff in the Prisoner's Dilemma (1.3.1)

u The probability of an immediate second interaction between two agents given a first (6.3.3)

$V\langle S_e \mid S_i \rangle$ The expected payoff to an individual playing strategy S_e against an individual using strategy S_i (2.3.1)

v The expected number of interactions (6.3.3) $\boldsymbol{v} = 1 / (1 - \boldsymbol{u})$

w The shadow of the future, also known as the discount parameter (1.3.2)

X_m The set of value pairs from all simulation runs at movement probability $\boldsymbol{m}$ (6.4.1)

$\overline{X}$ The set of all value pairs from all simulation runs at all movement probabilities studied (6.4.1)

X' The set of all averaged result pairs from two different models at all movement probabilities studied (6.4.1)

x The calculation of correlation on set $\overline{X}$ (6.4.1)

x' The calculation of correlation on set $\boldsymbol{X_m}$ for some movement probability $\boldsymbol{m}$ (6.4.1)

x'' The calculation of correlation on set $\boldsymbol{X}'$ (6.4.1)

$\boldsymbol{\mu}$ The point mutation probability (4.4)

$\boldsymbol{\chi}$ The parameterised crossover probability (4.4)

Appendix A – Investigating the Mechanisms Underlying Cooperation in Viscous Population Multi-Agent Systems

The following pages of this appendix contain a reproduction of the paper:

Marshall, J.A.R. & J.E. Rowe (2000). Investigating the Mechanisms Underlying Cooperation in Viscous Population Multi-Agent Systems. Artificial Life VII: Proceedings of the Seventh International Conference, edited by Mark A. Bedau, John S. McCaskill, Norman H. Packard, and Steen Rasmussen. MIT Press, 2000

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Investigating the Mechanisms Underlying Cooperation in Viscous Population Multi-Agent Systems

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Abstract

This paper presents a viscous population multi-agent system, which is claimed to provide scope for the emergence of cooperation both through iterated interaction and through kin selection. Theoretical examinations of iterated interaction and kin selection within the model are conducted and compared with empirical results. It is concluded that the model does allow for the operation both of iterated interaction and kin selection. The methods presented in the paper allow the operation of the two mechanisms to be distinguished in any instance of the model.

Introduction

The Prisoner's Dilemma (PD), first formalised by Tucker, is a well known metaphor for social interactions between individuals in which there is a dilemma over whether to act cooperatively or selfishly. In the single shot PD selfish behaviour is the only rational outcome (Nash 1950,1951). However (Axelrod 1984) proposed iterated interaction in the PD as a mechanism for promoting cooperation.

An alternative explanation for the evolution of cooperative behaviour in populations exists in (Hamilton 1964)'s theory of kin selection. Kin selection theory expects cooperative behaviour to be favoured in situations in which an individual's behaviour has an effect on the reproductive success of its relatives. In particular, so-called "viscous populations", in which individuals have limited dispersal and so tend to interact with relatives, provide such a situation. However, in these same populations, there is a potential force opposing the operation of kin selection, namely competition among relatives for finite resources.

Kin selection has previously been examined through computer simulation by (Oliphant 1994). Oliphant's model used genetic algorithms in a one-dimensional spatial environment to model individuals playing the non-iterated PD with their neighbours, and producing offspring within the same neighbourhoods. The results from the model showed that cooperation could emerge in such an environment through kin selection.

This paper presents a multi-agent evolutionary model with the PD as the model of social interaction. The model allows for the evolution of cooperation through kin selection as in (Oliphant 1994) as well as through iterated interaction. A mathematical investigation of the influence of repeated interaction and kin selection in the model is presented, and conclusions are drawn on empirical results in the light of these investigations.

The Model

The model described in this paper was implemented using the Swarm software from the Swarm Development Group (http://www.swarm.org). Source code for the model is available from one of the authors' websites (http://www.mk.dmu.ac.uk/~jmarshall).

Model Overview

The model used comprises a population of agents, and an environment in which they are situated. The environment is simply a grid of cells, with each edge of the grid wrapped around to meet its opposite edge, thus forming a torus. This type of toroidal environment has become widespread in artificial life models, such as that presented in (Nowak and May 1993). Each cell is capable of housing any number of agents from zero upwards. Cells are used as the local area of interaction, i.e. agents can only play the PD with, and mate with, agents in the cell they currently inhabit. At each time step, agents are able to move to any of the eight adjacent cells with a certain probability. In addition to this physical environment, there are eight environmental variables, namely the mutation rate, the parameterised crossover rate, the maximum population the environment can support, the initial population, the death probability, the movement probability, the initial agent energy, and the energy cost for living. These variables are described in the following sections.

Agent Description

Each agent is defined as having a chromosome, an energy level, and a memory of PD interactions with other agents.
For every other "opponent" that an agent has interacted with during its lifetime the agent remembers both the last actions of itself and its "opponent" (cooperate (C) or defect

(D) in each case). This memory is used to determine the action an agent will take next time it meets the same "opponent". The mapping of this interaction history to an action is achieved by the agent's strategy chromosome.

The agents' chromosomes specify characteristics of the agents, and are used during interaction and mating. These chromosomes are based on (Holland 1975)'s pioneering work using genetic algorithms in adaptive artificial systems.

Following (Mar and St. Denis 1994), a five loci chromosome is used, each locus having two alleles, a cooperation allele and a defection allele. This chromosome describes a "two-dimensional" strategy, which specifies a cooperate or defect action based on the previous action of each interacting individual. Four loci are used to specify actions based on this previous pair of interactions. The remaining locus is used to specify an initial action when the agent has never interacted with its opponent before.

Lastly, the agents also have an energy level, initialised at their "birth" and decreased by a certain amount every time step. Agents "die" when their energy level reaches zero, and the only way to replenish this energy and thus survive longer is by receiving payoffs from PD interactions with other agents. The PD payoffs used were temptation $T = 5$, reward $R = 3$, punishment $P = 1$ and sucker's payoff $S = 0$.

Model Operation

The operation of the model is now described. In the first stage an initial population is created, of a size specified by an environmental variable, and randomly distributed over the environment. Each agent's initial energy level is set to a specified level. In the second stage, each agent's energy level is decreased by the "living cost" specified. Any agent whose energy level reaches zero is removed from the population. The next stage terminates agents randomly according to the probability of death in the environment. These two methods of termination correspond to "death by starvation" and by "natural causes". In the fourth stage all the agents move to an adjacent cell with a certain probability. This probability can be changed to vary the population viscosity, the implications of which are discussed in the next section. Next, agents are randomly paired up within each cell, and each pair plays one round of the Prisoner's Dilemma. The action each agent chooses will be determined by their interaction history together, and their individual strategy chromosomes. As a result of this, agents' energy levels are increased in the next stage by the payoff received from the PD interaction. Finally the agents in a cell are again randomly paired, and produce offspring with a probability $1 - P$, where P is the proportion of the maximum possible population that the current population represents, and $0 <= P <= 1$. On completion of this stage the model re-enters the second stage and executes as before.

A pair of agents reproduce to combine their genetic material into one offspring agent, whose energy level is initialised appropriately. The genetic operators used in the reproduction process are (Spears and DeJong 1991)'s parameterised crossover operator, and a standard mutation operator.

Kin Selection

A Necessary Condition for Kin Selection

There is one fundamental condition for the operation of kin selection, that the behaviour of an individual has an effect on the reproductive success of its relatives (Hamilton 1964). Our model addresses this condition in two ways. First, the local random movement of agents leads to PD interactions among relatives, as a result of the agents' mating and interaction neighbourhoods being identical. Second, agents' behaviour has an effect on relatives' reproductive success, because payoffs from PD interactions are used as "energy" which is necessary for an agent's continued survival. Therefore exploitation of a relative (or indeed any other agent) will directly harm them by depriving them of vital "energy". This can directly contribute to their "death". The method of local interaction and mating described above creates what is termed a viscous population, which provides a suitable environment for kin selection to operate. As (Hamilton 1964) said, "we would expect to find giving traits commonest and most highly developed in the species with the most viscous populations whereas uninhibited competition should characterise species with the most freely mixing populations."

The Opposing Forces of Kin Selection

When considering kin selection as a potential explanation for cooperative behaviour, it is important to note the possible existence of mechanisms counter-acting its operation. Such a counteracting mechanism could exist in the form of competition between relatives for finite resources. (Wilson, Pollock and Dugatkin 1992) studied a viscous population model and concluded that the effects of these opposing mechanisms exactly cancelled each other, reducing evolutionary fitness to the simplest form of individual fitness. (Taylor 1992a) concluded the same for homogenous environments, as well as extending their results to patch-structured populations (Taylor 1992b). However others, such as (Kelly 1992,1994) and (Queller 1994), argued against these claims. (Kelly 1994) in particular suggested that regulation of a population at the global rather than local level would still allow kin selection to be effective. The model studied in this paper implements such global population regulation.

Examination of the Implicit Shadow of the Future

Based on the model described above, it is possible to make some simple calculations about the probability of repeated interaction between two agents. Due to the undecidability

inherent in such models (Grim 1994), even those without stochastic elements, these are limited to calculations from one time step to the next. However, we can still use these calculations to get an impression of the implicit "shadow of the future" (Axelrod 1984). The shadow of the future is defined as the probability that two agents will interact again at some point in the future. If the shadow of the future is large then iterated interaction is likely, and so cooperation is favoured. If, however, the shadow of the future is small, then single iteration encounters are common, and so defection is favoured.

The following equation calculates the probability of two consecutive interactions between the same agents, where m represents the agents' movement probability, d the environmental death probability, and p the size of the local population in an agent's cell. It should be noted that it is difficult to take into account the probability of an agent's death through running out of energy.

$$\frac{(1-d)^2}{(p-1)}\left((1-m)^2+\frac{m^2}{8}\right)$$

Repeated interaction in the model is a geometric process, ignoring death by "starvation". Given one interaction, the probability there will be another is $1/(1-q)$, where q is the repeated interaction probability from the previous formula.

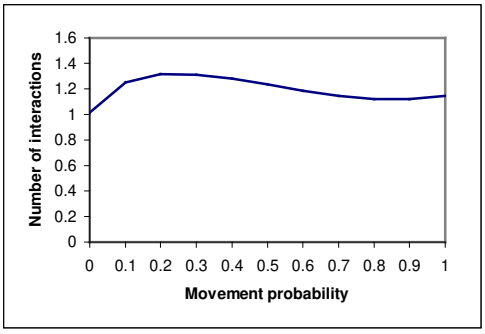

Figure 1. Expected number of interactions between agent pairs, under varying movement probability

The results of this calculation are presented in figure 1 above. The parameters used to draw this graph are: d = 0.05. As local population level p varies according to movement probability m in the model, the value for p at each value of m was taken from empirical data gathered from the model.

Examination of Inclusive Fitness of Cooperation and Defection Alleles

Not all the loci on an agent's chromosome are subject to kin selection. Some loci are used only in interactions where both agents will see the same interaction history and therefore use the same locus to determine their actions. Hence kin selection cannot operate on these loci. However interactions using the remaining loci will always result in each interacting agent using a different locus to determine their action. At these loci alleles can benefit copies of themselves in an "opponent" agent through increasing the fitness of the "opponent" agent, possibly at the expense of agent in which they are carried. For these loci it is interesting to calculate the inclusive fitness of cooperation and defection alleles, to gain a greater understanding of the potential for the operation of kin selection within the model. This calculation is presented below. In the following equations, T, R, S and P represent the payoffs in the Prisoner's Dilemma, c represents the frequency of cooperators in the environment, r represents the relatedness of the agents at the locus of the allele whose fitness we are considering.

Inclusive fitness of cooperation allele:

$$(Rc + S(1 - c)) + ((Rc + T(1 - c))r)$$

Inclusive fitness of defection allele:

$$(Tc + P(1 - c)) + ((Sc + P(1 - c))r)$$

In each of these equations, the first term represents the fitness of the allele in one interacting agent, the second term represents the fitness of a copy of that allele in its "opponent" agent, multiplied by a coefficient of relatedness. This is the standard inclusive fitness calculation (Hamilton 1964), interpreting payoff from a Prisoner's Dilemma interaction as reproductive potential. Each fitness term is calculated as the average payoff received by the agent weighted by the frequency of cooperators in the environment (i.e. the probability that an agent's "opponent" will cooperate in an interaction).

These two equations were used to draw the graph shown below in figure 2, given the following parameters: T = 5, R = 3, S = 0, P = 1.

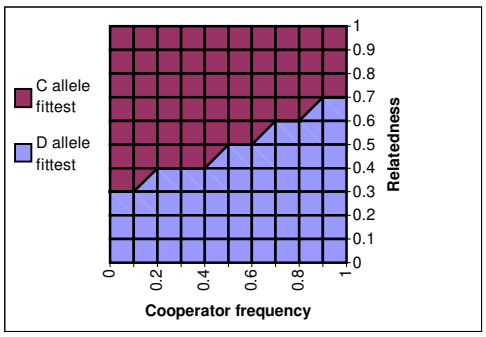

Figure 2. Relative fitness of cooperation and defection alleles at loci subject to kin selection

The inclusive fitness results in figure 2 above clearly show that the model supports kin selection. This can be seen by observing that, for the loci we are considering, the C allele is fittest at high relatedness levels.

Presentation and Discussion of Results

Experiments were run to observe the effect of varying population viscosity in the model, through changing the movement probability of agents, as follows: the experiments were conducted in 11 parameter configurations, sweeping the movement probability from 0 to 1 inclusive in increments of 0.1. For each parameter

configuration 20 runs of 1000 time steps each were conducted. For each run, the average cooperation over the entire run was calculated, and this was used to calculate the average and standard deviation of the cooperation level for each value of the movement probability. The average number of interactions between any two interacting agents was also calculated, as well as the average relatedness of interacting agent pairs. Relatedness was calculated using the following formula from (Collins and Jefferson 1991), where f_i = frequency of allele 1 (for example) at locus i, l = number of loci being compared and $0 \le D \le 1$. The relatedness of two interacting agents was therefore calculated as 1-D, with $l = 5$.

$$D = \frac{\sum_{i=1}^{l}(1 - 4(0.5 - f_i)^2)}{l}$$

The other model parameters were as follows: environment width and height = 10, maximum agent population = 200, initial agent population = 75, mutation rate = 0.01, parameterised crossover rate = 0.1, death probability = 0.05, initial agent energy = 15, living cost = 3.

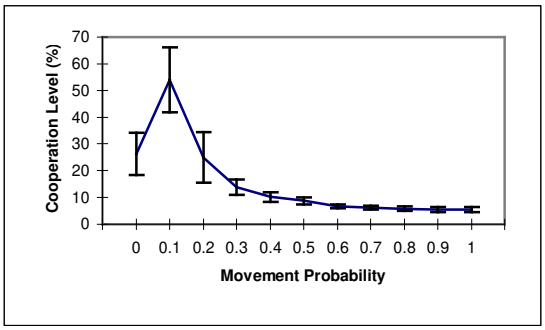

Figure 3. Global cooperation level among all agents in model

In figure 3 the cooperation level, averaged globally over all types of interaction, behaves as predicted both by iterated interaction and kin selection theory, increasing as population viscosity increases (agent movement probability decreases). It is interesting to note, however, that cooperation levels remain low across all movement probabilities, only approaching the mean at the lowest movement probabilities.

Figure 4 below presents the average number of interactions within agent pairs in the experiment, while figure 5 presents the average relatedness of pairs of interacting agents.

In figure 4, average number of interactions could be considered to be well correlated with average cooperation level in the model. Both values exhibit the same increase under decreasing movement probability, peaking at movement probability 0.1, subsequently falling at movement probability 0. In fact the only obvious difference between the curves of average cooperation level and average interaction length is the magnitude of fall at movement probability 0.

Comparing the theoretical predictions shown in figure 1 with the empirical results presented in figure 4, it can be seen that there is a close match, apart from some discrepancies at movement probabilities 0.1 and 0.2. It is suggested that the reason for these discrepancies is that the theoretical calculations cannot take account of death by "starvation", which may become increasingly important at the lower movement probabilities.

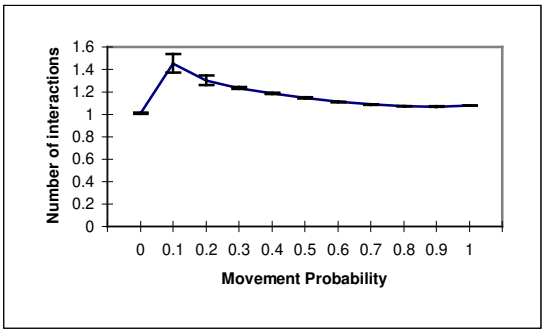

Figure 4. Average number of interactions within agent pairs

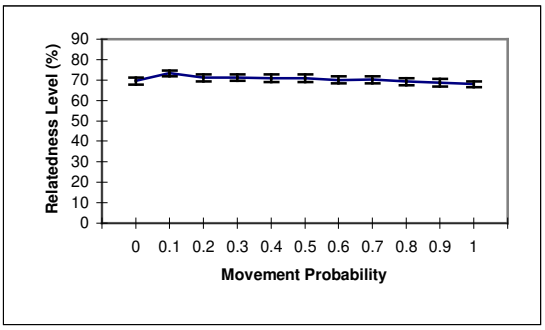

Figure 5. Average relatedness of interacting agent pairs

Figure 5 shows a high degree of relatedness within interacting agent pairs. However this relatedness level is comparatively constant over movement probability.

In addition to these results, further cooperation and relatedness data was collected from the experiments, focussing on a subset of the initial data. Figure 6 and figure 7 below present the average cooperation level and relatedness of agent pairs respectively, for interactions determined by the two loci subject to kin selection. The motivation for studying this subset of the data was presented in the section entitled "Examination of Inclusive Fitness of Cooperation and Defection Alleles".

Figure 6 shows a noisy cooperation level that does not vary with movement probability, but remains around the mean cooperation level found in the absence of selection.

Figure 7 shows the same high relatedness level observed in figure 5. It is interesting to note that while relatedness does increase as population viscosity increases (movement probability decreases), this increase is not as pronounced as (Hamilton 1964) suggested it might be. Possible explanations for this may include the existence of forces counteracting the operation of kin selection, as outlined under the heading "The Opposing Forces of Kin Selection". Alternatively, the particular parameters used for the experiments, more particularly the PD parameters, may not allow kin selection to operate effectively. This is

suggested by the cooperation levels presented in figure 6, which are based around the mean cooperation level found in the absence of selection, and do not show any trend over varying movement probability.

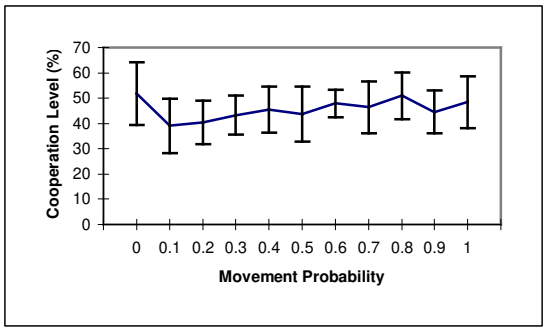

Figure 6. Average cooperation level for interactions using loci subject to kin selection

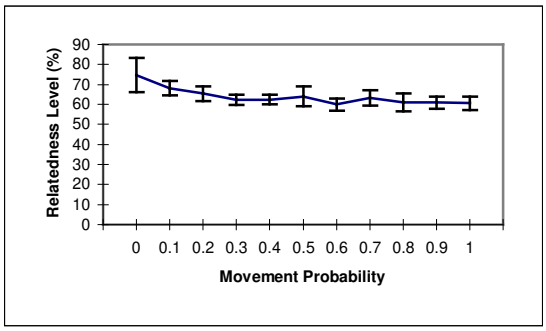

Figure 7. Average relatedness of interacting agent pairs for interactions using loci subject to kin selection

Returning to the theoretical result presented in figure 2, and taking the empirical relatedness level from figure 7, we can suggest an explanation for the observed mean cooperation level by examining the parameter space of relative C and D allele fitness. Looking at figure 2 with a relatedness level of between 0.6 and 0.7 (taken from figure 7), we find at cooperator frequencies 0.7 to 1 the threshold of relative C allele/D allele fitness. There is little difference between the fitness of the C and D alleles at this point in the parameter space, thus there is an absence of strong selection on these loci, resulting in the mean cooperation level observed.

Conclusions

This paper has presented a theoretical examination of the possible mechanisms underlying emergent cooperation in a viscous population multi-agent system. These examinations, in conjunction with empirical data from the model, conclude that the model presented allows for cooperation to emerge both through iterated interaction and through kin selection. The methods presented allow for the differentiation of the two mechanisms underlying cooperation in different cases of the presented model.

Acknowledgements

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Appendix B – Objective C Source for the Evolutionary Prisoner's Dilemma

This appendix includes the Objective C source files for the Evolutionary Prisoner's Dilemma, and the `Makefile` needed to compile them. The mode that the Evolutionary Prisoner's Dilemma is compiled in is controlled by `EPDDefines.h`. The experimental parameters of the Evolutionary Prisoner's Dilemma are controlled by `experiment.setup`, `payoffs.setup` and `world.setup`. The Evolutionary Prisoner's Dilemma requires Swarm version 2.1.1 to be installed in order to compile and execute.

Makefile

```
SWARMHOME=C:/Swarm-2.1.1/
APPLICATION=EPD
OBJECTS=main.o EPDExperimentSwarm.o EPDObserverSwarm.o EPDSwarm.o EPDWorld.o
EPDAgent.o DoubleData.o IntegerData.o
include $(SWARMHOME)/etc/swarm/Makefile.appl

main.o: main.m EPDExperimentSwarm.h EPDObserverSwarm.h EPDSwarm.h EPDWorld.h
EPDAgent.h DoubleData.h IntegerData.h EPDDefines.h
EPDExperimentSwarm.o: EPDExperimentSwarm.h EPDExperimentSwarm.m EPDSwarm.h
EPDObserverSwarm.o: EPDObserverSwarm.h EPDObserverSwarm.m EPDSwarm.h EPDDefines.h
EPDSwarm.o: EPDSwarm.h EPDSwarm.m EPDWorld.h EPDDefines.h
EPDWorld.o: EPDWorld.h EPDWorld.m IntegerData.h DoubleData.h EPDDefines.h
EPDAgent.o: EPDAgent.h EPDAgent.m EPDWorld.h DoubleData.h EPDDefines.h
DoubleData.o: DoubleData.h DoubleData.m
IntegerData.o: IntegerData.h IntegerData.m
```

EPDDefines.h

```
//EPDDefines.h

#define observer //define for observer mode of application, undefine for experiment
mode
#define global_population_regulation //  if defined population is regulated at global
level, otherwise at local (cell) level
//#define global_mating_pool // if defined mating and offspring distribution is global
rather than local
//#define pure_kin_selection //if defined special version of model to study pure kin
selection, with one-dimensional agent strategies (2 locus chromosomes) and roles
randomly assigned at meetings
//only one of the interaction method constants below should be defined
#define interaction_method1 //one PD interaction at each meeting (not valid if
pure_kin_selection defined)
//#define interaction_method2 //three PD interactions at each meeting (DO NOT DEFINE
IF pure_kin_selection DEFINED)
//only one of the first 3 relatedness measure contants below should be defined
//#define relatedness_measure1 //global relatedness measured on global population
//#define relatedness_measure2 //global relatedness measured as average of populated
cells' local relatedness
#define relatedness_measure3 //global relatedness measured on interacting pairs
//#define relatedness_measure4 //IF DEFINED IN CONJUNCTION WITH relatedness_measure3:
global relatedness calculated only on merciful/exploitative and forgiving/vengeful
loci (DO NOT DEFINE IF pure_kin_selection DEFINED)
//#define consider_interaction_subset //update cooperation level and relatedness level
only for interactions involving merciful/exploitative and forgiving/vengeful loci (DO
NOT DEFINE IF pure_kin_selection DEFINED)
//#define role_swap_cooperation //measure cooperation on instances of agents using
different roles (for use with Battle of the Sexes payoff matrix)

//error checking
#if defined(interaction_method1) && defined(interaction_method2)
  #error
```

```
#endif
#if (defined(relatedness_measure1) && defined(relatedness_measure2)) ||
(defined(relatedness_measure1) && defined(relatedness_measure3)) ||
(defined(relatedness_measure2) && defined(relatedness_measure3))
  #error
#endif
#if defined(pure_kin_selection) && (defined(relatedness_measure4) ||
defined(consider_interaction_subset) || defined(interaction_method2))
  #error
#endif
#if defined(relatedness_measure4) && !defined(relatedness_measure3)
  #error
#endif
```

main.m

```
//main.m EPD

#import "EPDDefines.h"
#ifdef observer
  #import "EPDObserverSwarm.h"
#else
  #import "EPDExperimentSwarm.h"
#endif
#import <simtools.h>

int main(int argc,const char **argv)
{
  id epdObserverSwarm;

  initSwarm(argc,argv);

  //make the model swarm
  #ifdef observer
    epdObserverSwarm=[EPDObserverSwarm create: globalZone];
  #else
    epdObserverSwarm=[EPDExperimentSwarm create: globalZone];
  #endif

  //send messages to swarm to create internal objects and activities
  [epdObserverSwarm buildObjects];
  [epdObserverSwarm buildActions];

  //activate the swarm
  [epdObserverSwarm activateIn: nil];

  //run the swarm
  [epdObserverSwarm go];
  return 0;
}
```

EPDExperimentSwarm.h

```
// EPDExperimentSwarm.h

#import "EPDSwarm.h"

#import <gui.h>
#import <simtoolsgui.h>
#import <simtoolsgui/GUISwarm.h>
#import <analysis.h>

@interface ParameterManager: SwarmObject
{
  double movementProbability, moveProbInc, moveProbMax;
  int runNumber, runNumberMax;

  id pmProbeMap;
}

- initializeParameters;
- initializeModel: (id)theModel;
- stepParameters;
- printParameters: anOutFile;
```

```
@end

@interface EPDExperimentSwarm: GUISwarm
{
  int modelTime, averageCooperation, averageRelatedness, numModelRuns;
  double averageInteractionLength, averageCellPopulation, averageNumberOfPartners;

  id modelProbeMap;
  id displayActions;
  id displaySchedule;
  id epdSwarm, parameterManager, logFile;

//  EZGraph *resultGraph;
}

+createBegin: (id) aZone;
-createEnd;

-buildObjects;
-buildActions;
-activateIn: (id) swarmContext;

@end
```

EPDExperimentSwarm.m

```
//EPDExperimentSwarm.m

#import "EPDExperimentSwarm.h"

@implementation ParameterManager

  // The ParameterManager handles the parameter manipulation for
  //     the series of models run during the experiment


- initializeParameters
{
  //create the probe map for the parameter manager
  pmProbeMap = [EmptyProbeMap createBegin: [self getZone]];
  [pmProbeMap setProbedClass: [self class]];
  pmProbeMap = [pmProbeMap createEnd];

  //add probes for the parameter manager's variables
  [pmProbeMap addProbe: [probeLibrary getProbeForVariable: "movementProbability"
inClass: [self class]]];
  [pmProbeMap addProbe: [probeLibrary getProbeForVariable: "moveProbInc" inClass:
[self class]]];
  [pmProbeMap addProbe: [probeLibrary getProbeForVariable: "moveProbMax" inClass:
[self class]]];
  [pmProbeMap addProbe: [probeLibrary getProbeForVariable: "runNumber" inClass: [self
class]]];
  [pmProbeMap addProbe: [probeLibrary getProbeForVariable: "runNumberMax" inClass:
[self class]]];

  //set the probe map for the parameter manager
  [probeLibrary setProbeMap: pmProbeMap For: [self class]];

  //load parameters from file 'experiment.setup'
  [ObjectLoader load: self fromFileNamed: "experiment.setup"];

  //create display for parameter manager probe
  [probeDisplayManager createProbeDisplayFor: self];

  return self;
}

- initializeModel: (id)theModel
{
  [theModel setMoveProbability: movementProbability]; //set the movement probability
for agents in the model

  return self;
}
```

```
- stepParameters
{
  runNumber++; //increment the run number for the current parameter settings
  //sweep to the next parameter values and reset the run number if the all the runs
have completed for these values
  if (runNumber>runNumberMax)
  {
    runNumber=1;
    movementProbability += moveProbInc;

    if (movementProbability > moveProbMax)
    {
      return nil;
    }
  }

  return self;
}

- printParameters: (id <OutFile>)anOutFile
{
  //store the parameter values in a file
  [anOutFile putNewLine];
  [ObjectSaver save: self to: anOutFile withTemplate: pmProbeMap];
  [anOutFile putNewLine];

  return self;
}

@end

@implementation EPDExperimentSwarm

+createBegin: (id) aZone
{
  EPDExperimentSwarm *obj;
  id <ProbeMap> probeMap;

  obj=[super createBegin: aZone];

  //create the probe map for the experiment Swarm
  probeMap=[EmptyProbeMap createBegin: aZone];
  [probeMap setProbedClass: [self class]];
  probeMap=[probeMap createEnd];

  //set the probe map for the experiment Swarm
  [probeLibrary setProbeMap: probeMap For: [self class]];

  return obj;
}

-createEnd
{
  return [super createEnd];
}

-buildObjects
{
  id modelZone;

  [super buildObjects];

  //create the parameter manager
  parameterManager=[ParameterManager create: self];
  [parameterManager initializeParameters];

  //create the Swarm
  modelZone=[Zone create: [self getZone]];
  epdSwarm=[EPDSwarm create: modelZone];

  //create the display for the experiment Swarm probe
  [probeDisplayManager createProbeDisplayFor: self];

  [controlPanel setStateRunning];
```

```
  //create the log file
  logFile=[OutFile create: self setName: "log.file"];

  return self;
}

-buildActions
{
  [super buildActions];

  displayActions=[ActionGroup create: [self getZone]];

  //create the action group to build and run the models and log results
  [displayActions createActionTo: self message: M(buildModel)];
  [displayActions createActionTo: self message: M(runModel)];
  [displayActions createActionTo: self message: M(doStats)];
  [displayActions createActionTo: self message: M(showStats)];
  [displayActions createActionTo: self message: M(logResults)];
  [displayActions createActionTo: self message: M(dropModel)];
  [displayActions createActionTo: self message: M(checkToStop)];

  [displayActions createActionTo: probeDisplayManager message: M(update)];

  [displayActions createActionTo: actionCache message: M(doTkEvents)];

  //create the schedule to execute the action group
  displaySchedule=[Schedule createBegin: [self getZone]];
  [displaySchedule setRepeatInterval: 1];
  displaySchedule=[displaySchedule createEnd];

  //schedule the action group
  [displaySchedule at: 0 createAction: displayActions];

  return self;
}

-activateIn: (id)swarmContext
{
  [super activateIn: swarmContext];

  [epdSwarm activateIn: self];

  [displaySchedule activateIn: self];

  return [self getSwarmActivity];
}

- buildModel
{
  //create the model Swarm
  epdSwarm = [EPDSwarm create: self];

  // If this is the first model, create a custom probeMap for modelSwarm
  // and construct a graph displaying model results

  if (numModelRuns == 0)
    {
      modelProbeMap = [EmptyProbeMap createBegin: self];
      [modelProbeMap setProbedClass: [EPDSwarm class]];
      modelProbeMap = [modelProbeMap createEnd];

      [modelProbeMap addProbe: [probeLibrary getProbeForVariable: "worldXsize"
inClass: [EPDSwarm class]]];
      [modelProbeMap addProbe: [probeLibrary getProbeForVariable: "worldYsize"
inClass: [EPDSwarm class]]];
      [modelProbeMap addProbe: [probeLibrary getProbeForVariable: "maxAgents" inClass:
[EPDSwarm class]]];
      [modelProbeMap addProbe: [probeLibrary getProbeForVariable: "maxLocalAgents"
inClass: [EPDSwarm class]]];
      [modelProbeMap addProbe: [probeLibrary getProbeForVariable: "startAgents"
inClass: [EPDSwarm class]]];
      [modelProbeMap addProbe: [probeLibrary getProbeForVariable: "deathProbability"
inClass: [EPDSwarm class]]];
      [modelProbeMap addProbe: [probeLibrary getProbeForVariable: "moveProbability"
inClass: [EPDSwarm class]]];
      [modelProbeMap addProbe: [probeLibrary getProbeForVariable: "mutationRate"
inClass: [EPDSwarm class]]];
```

```
      [modelProbeMap addProbe: [probeLibrary getProbeForVariable: "crossProbability"
inClass: [EPDSwarm class]]];
      [modelProbeMap addProbe: [probeLibrary getProbeForVariable: "startEnergy"
inClass: [EPDSwarm class]]];
      [modelProbeMap addProbe: [probeLibrary getProbeForVariable: "livingCost"
inClass: [EPDSwarm class]]];

      [probeLibrary setProbeMap: modelProbeMap For: [EPDSwarm class]];

  }

  //initialise the model Swarm according to the values in the parameter manager
  [parameterManager initializeModel: epdSwarm];

  //build and activate the model swarm
  [epdSwarm buildObjects];
  [epdSwarm buildActions];
  [epdSwarm activateIn: nil];

  return self;
}


- runModel
{
  printf("\nStarting model %d \n", numModelRuns+1);

  [[epdSwarm getActivity] run];

  printf("Model %d is done \n", numModelRuns+1);

  numModelRuns++;

  return self;
}


- doStats
{
  //display the model run results on standard output
  modelTime =  [[epdSwarm getWorld] getWorldTime];
  averageCooperation=[[epdSwarm getWorld] getAverageCooperationLevel];
  averageRelatedness=[[epdSwarm getWorld] getAverageRelatedness];
  averageInteractionLength=[[epdSwarm getWorld] getAverageInteractionLength];
  averageCellPopulation=[[epdSwarm getWorld] getAverageLocalPopSize];
  averageNumberOfPartners=[[epdSwarm getWorld] getAverageNumberOfPartners];

  printf("Length of this run = %d \n", modelTime);
  printf("Movement probability = %f\n",[[epdSwarm getWorld] getMoveProbability]);
  printf("Average cooperation = %d\n", averageCooperation);
  printf("Average relatedness = %d\n", averageRelatedness);
  printf("Average interaction length = %f\n", averageInteractionLength);
  printf("Average cell population = %f\n", averageCellPopulation);
  printf("Average number of partners per agent = %f\n", averageNumberOfPartners);

  return self;
}


- (int)getModelTime
{
  // This method feeds the EZGraph "runTime" sequence
  // this always points to the current modelSwarm

   return [[epdSwarm getWorld] getWorldTime];
}


- logResults
{
  //store the model run results in the log file
  [logFile putInt: averageCooperation];
  [logFile putString: ","];
  [logFile putInt: averageRelatedness];
  [logFile putString: ","];
  [logFile putDouble: averageInteractionLength];
  [logFile putString: ","];
```

```
  [logFile putInt: modelTime];
  [logFile putString: ","];
  [logFile putDouble: averageCellPopulation];
  [logFile putString: ","];
  [logFile putDouble: averageNumberOfPartners];
  [logFile putNewLine];

  return self;
}


- showStats
{
//  [resultGraph step];
  return self;
}


- dropModel
{
  [[epdSwarm getActivity] drop];
  [epdSwarm drop];

  return self;
}


- checkToStop
{
  //check if the current model run has reached the termination point (defined as an
execution length)
  if ([parameterManager stepParameters]==nil)
    {
      [probeDisplayManager update];
      [actionCache doTkEvents];

      printf("\n All the models have run!\n");

      [logFile drop];
      [controlPanel setStateQuit];
    }

  return self;
}

@end
```

EPDObserverSwarm.h

```
// EPDObserverSwarm.h

#import "EPDSwarm.h"

#import <gui.h>
#import <simtoolsgui/GUISwarm.h>
#import <simtoolsgui.h>
#import <analysis.h>

@interface EPDObserverSwarm: GUISwarm
{
  int displayFrequency;
  id displayActions;
  id displaySchedule;
  id epdSwarm;
  id <Colormap> worldColourMap, populationColourMap;
  id <ZoomRaster> worldRaster, populationRaster;
  id <Value2dDisplay> worldValueDisplay, populationValueDisplay;
  id <EZGraph> coopGraph, alleleGraph;
}

+createBegin: (id) aZone;
-createEnd;

-buildObjects;
-buildActions;
```

```
-activateIn: (id) swarmContext;

@end
```

EPDObserverSwarm.m

```
//EPDObserverSwarm.m

#import "EPDObserverSwarm.h"

@implementation EPDObserverSwarm

+createBegin: (id) aZone
{
  EPDObserverSwarm *obj;
  id <ProbeMap> probeMap;

  obj=[super createBegin: aZone];
  obj->displayFrequency=1;

  //create the probe map for the observer Swarm
  probeMap=[EmptyProbeMap createBegin: aZone];
  [probeMap setProbedClass: [self class]];
  probeMap=[probeMap createEnd];

  //add a probe for display frequency to the probe map, and set the probe map for the
observer Swarm
  [probeMap addProbe: [probeLibrary getProbeForVariable: "displayFrequency" inClass:
[self class]]];
  [probeLibrary setProbeMap: probeMap For: [self class]];

  return obj;
}

-createEnd
{
  return [super createEnd];
}

-buildObjects
{
  id modelZone;
  int l1,l2, zf;

  [super buildObjects];

  //create the model Swarm
  modelZone=[Zone create: [self getZone]];
  epdSwarm=[EPDSwarm create: modelZone];

  //create the probe displays for the model and observer Swarms
  [probeDisplayManager createProbeDisplayFor: epdSwarm];
  [probeDisplayManager createProbeDisplayFor: self];

  [controlPanel setStateStopped];

  //build the objects in the model Swarm
  [epdSwarm buildObjects];

  //create a colour map (grey scale) for displaying cell population densities
  populationColourMap=[Colormap create: modelZone];
  [populationColourMap setColor: 0 ToName: "blue"];
  for (l1=1; l1<=10; l1++)
  {
    [populationColourMap setColor: l1 ToGrey: (double)l1/10];
  }

  //create a colour map for displaying cell cooperation and relatedness levels
  worldColourMap=[Colormap create: modelZone];
  [worldColourMap setColor: 0 ToName: "black"];
  for (l1=0; l1<=10; l1++)
  {
    for (l2=0; l2<=10; l2++)
    {
```

```
      [worldColourMap setColor: (l1*11)+l2+1 ToRed: (double)l1/10 Green: (double)l2/10
Blue: (double)1];
    }
  }
  [worldColourMap setColor: 122 ToRed: 1 Green: 0 Blue: 0]; //red for individual
agents

  //create a raster object for displaying cell population densities
  zf=500/[epdSwarm getWorldXSize];
  if (zf>50)
  {
    zf=50;
  }

  populationRaster=[ZoomRaster create: modelZone];
  [populationRaster setColormap: populationColourMap];
  [populationRaster setZoomFactor: zf];
  [populationRaster setWidth: [epdSwarm getWorldXSize] Height: [epdSwarm
getWorldYSize]];
  [populationRaster setWindowTitle: "EPD Population"];
  [populationRaster drawSelf];
  [populationRaster pack];

  //create a raster object for displaying cell cooperation and relatedness levels
  worldRaster=[ZoomRaster create: modelZone];
  [worldRaster setColormap: worldColourMap];
  [worldRaster setZoomFactor: zf];
  [worldRaster setWidth: [epdSwarm getWorldXSize] Height: [epdSwarm getWorldYSize]];
  [worldRaster setWindowTitle: "EPD World"];
  [worldRaster drawSelf];
  [worldRaster pack];

  //create a display object for cell population densities
  populationValueDisplay=[Value2dDisplay createBegin: [self getZone]];
  [populationValueDisplay setDisplayWidget: populationRaster colormap:
populationColourMap];
  [populationValueDisplay setDiscrete2dToDisplay: [epdSwarm getPopulationDisplay]];
  populationValueDisplay=[populationValueDisplay createEnd];
  [populationValueDisplay setDisplayMappingM: 1 C: 0];

  //create a display object for cell cooperation and relatedness levels
  worldValueDisplay=[Value2dDisplay createBegin: [self getZone]];
  [worldValueDisplay setDisplayWidget: worldRaster colormap: worldColourMap];
  [worldValueDisplay setDiscrete2dToDisplay: [epdSwarm getWorldDisplay]];
  worldValueDisplay=[worldValueDisplay createEnd];
  [worldValueDisplay setDisplayMappingM: 1 C: 0];

  //create a graph object to display global cooperation and relatedness levels
  coopGraph=[EZGraph createBegin: [self getZone]];
  [coopGraph setTitle: "Cooperation & Relatedness vs time"];
  [coopGraph setAxisLabelsX: "time" Y: "level (%)"];
  coopGraph=[coopGraph createEnd];
  [coopGraph createSequence: "Cooperation level" withFeedFrom: [epdSwarm getWorld]
andSelector: M(getCoopLevel)];
  [coopGraph createSequence: "Global relatedness" withFeedFrom: [epdSwarm getWorld]
andSelector: M(getGlobalRelatedness)];

  //create a graph object to display allele frequencies in the gene pool
  alleleGraph=[EZGraph createBegin: [self getZone]];
  [alleleGraph setTitle: "Allele frequencies in population"];
  [alleleGraph setAxisLabelsX: "time" Y: "Level"];
  alleleGraph=[alleleGraph createEnd];
  [alleleGraph createSequence: "Total population" withFeedFrom: [epdSwarm getWorld]
andSelector: M(getWorldPopulation)];
  #ifdef pure_kin_selection
    [alleleGraph createSequence: "C allele (locus 0)" withFeedFrom: [[epdSwarm
getWorld] getAlleleFrequency: 0] andSelector: M(getIntData)];
    [alleleGraph createSequence: "C allele (locus 1)" withFeedFrom: [[epdSwarm
getWorld] getAlleleFrequency: 1] andSelector: M(getIntData)];
  #else
    [alleleGraph createSequence: "Friendly allele" withFeedFrom: [[epdSwarm getWorld]
getAlleleFrequency: 0] andSelector: M(getIntData)];
    [alleleGraph createSequence: "Constructive allele" withFeedFrom: [[epdSwarm
getWorld] getAlleleFrequency: 1] andSelector: M(getIntData)];
    [alleleGraph createSequence: "Merciful allele" withFeedFrom: [[epdSwarm getWorld]
getAlleleFrequency: 2] andSelector: M(getIntData)];
```

```
    [alleleGraph createSequence: "Forgiving allele" withFeedFrom: [[epdSwarm getWorld]
getAlleleFrequency: 3] andSelector: M(getIntData)];
    [alleleGraph createSequence: "Dovish allele" withFeedFrom: [[epdSwarm getWorld]
getAlleleFrequency: 4] andSelector: M(getIntData)];
  #endif

  return self;
}

-buildActions
{
  [super buildActions];

  //create the model Swarm's actions
  [epdSwarm buildActions];

  //create the action group to update the graphs and displays, and respond to user
events
  displayActions=[ActionGroup create: [self getZone]];
  [displayActions createActionTo: worldValueDisplay message: M(display)];
  [displayActions createActionTo: populationValueDisplay message: M(display)];
  [displayActions createActionTo: worldRaster message: M(drawSelf)];
  [displayActions createActionTo: populationRaster message: M(drawSelf)];
  [displayActions createActionTo: coopGraph message: M(step)];
  [displayActions createActionTo: alleleGraph message: M(step)];
  [displayActions createActionTo: actionCache message: M(doTkEvents)];

  //create the schedule to execute the action group with a certain display frequency
  displaySchedule=[Schedule createBegin: [self getZone]];
  [displaySchedule setRepeatInterval: displayFrequency];
  displaySchedule=[displaySchedule createEnd];

  //schedule the action group
  [displaySchedule at: 0 createAction: displayActions];

  return self;
}

-activateIn: (id)swarmContext
{
  [super activateIn: swarmContext];

  [epdSwarm activateIn: self];

  [displaySchedule activateIn: self];

  return [self getSwarmActivity];
}

@end
```

EPDSwarm.h

```
//EPDSwarm.h EPD

#import "EPDWorld.h"

#import <objectbase/Swarm.h>
#import <space.h>
#import <activity.h>
#import <random.h>
#import <collections.h>
#import <simtools.h>
#import "EPDDefines.h"

//#define debug

@interface Payoffs: SwarmObject
{
  int AAPayoff, ABPayoff, BAPayoff, BBPayoff;
}

-create;
-(int)getAAPayoff;
-(int)getABPayoff;
```

```
-(int)getBAPayoff;
-(int)getBBPayoff;

@end

@interface EPDSwarm: Swarm
{
  int worldXsize, worldYsize;
  int maxAgents, maxLocalAgents, startAgents, strategyLength;
  int startEnergy, livingCost;
  int endTime;
  double deathProbability, moveProbability;
  float mutationRate, crossProbability;
  id payoffs;

  id world;
  id populationDisplay, worldDisplay;
//  id <ListIndex> allAgents;
  id allAgents;
  id modelStep;
  id modelSchedule;
}

+createBegin: (id) aZone;
-createEnd;
-(void)drop;
-buildObjects;
-buildActions;
-activateIn: (id) swarmContext;
-getPopulationDisplay;
-getWorldDisplay;
-getWorld;
-(int)getWorldXSize;
-(int)getWorldYSize;
-setMoveProbability: (double) moveProb;
-checkToStop;

@end
```

EPDSwarm.m

```
//EPDSwarm.m EPD

#import "EPDSwarm.h"

@implementation Payoffs

-create
{
  AAPayoff=0;
  ABPayoff=0;
  BAPayoff=0;
  BBPayoff=0;

  return self;
}

-(int)getAAPayoff
{
  return AAPayoff;
}

-(int)getABPayoff
{
  return ABPayoff;
}

-(int)getBAPayoff
{
  return BAPayoff;
}

-(int)getBBPayoff
{
  return BBPayoff;
```

```
}

@end

@implementation EPDSwarm

+createBegin: (id) aZone
{
  EPDSwarm *obj;
#ifdef observer
  id <ProbeMap> probeMap;
#endif

  obj=[super createBegin: aZone];

  //initialise model Swarm parameters
  obj->worldXsize=10;
  obj->worldYsize=10;
  obj->maxAgents=200;
  obj->maxLocalAgents=5;
  obj->startAgents=75;
  #ifdef pure_kin_selection
    obj->strategyLength=2;
  #else
    obj->strategyLength=5;
  #endif
  obj->deathProbability=0.05;
  obj->moveProbability=1;
  obj->mutationRate=0.01;
  obj->crossProbability=0.1;
  #ifdef interaction_method1
    obj->startEnergy=9;
    obj->livingCost=3;
  #else
    obj->startEnergy=45;
    obj->livingCost=15;
  #endif
  obj->endTime=1000;

  #ifdef observer
    //create probe map for model Swarm
    probeMap=[EmptyProbeMap createBegin: aZone];
    [probeMap setProbedClass: [self class]];
    probeMap=[probeMap createEnd];

    //add probes for variables in model Swarm
    [probeMap addProbe: [probeLibrary getProbeForVariable: "worldXsize" inClass: [self
class]]];
    [probeMap addProbe: [probeLibrary getProbeForVariable: "worldYsize" inClass: [self
class]]];
    [probeMap addProbe: [probeLibrary getProbeForVariable: "maxAgents" inClass: [self
class]]];
    [probeMap addProbe: [probeLibrary getProbeForVariable: "maxLocalAgents" inClass:
[self class]]];
    [probeMap addProbe: [probeLibrary getProbeForVariable: "startAgents" inClass:
[self class]]];
    [probeMap addProbe: [probeLibrary getProbeForVariable: "deathProbability" inClass:
[self class]]];
    [probeMap addProbe: [probeLibrary getProbeForVariable: "moveProbability" inClass:
[self class]]];
    [probeMap addProbe: [probeLibrary getProbeForVariable: "mutationRate" inClass:
[self class]]];
    [probeMap addProbe: [probeLibrary getProbeForVariable: "crossProbability" inClass:
[self class]]];
    [probeMap addProbe: [probeLibrary getProbeForVariable: "startEnergy" inClass:
[self class]]];
    [probeMap addProbe: [probeLibrary getProbeForVariable: "livingCost" inClass: [self
class]]];
    [probeMap addProbe: [probeLibrary getProbeForVariable: "endTime" inClass: [self
class]]];
    [probeLibrary setProbeMap: probeMap For: [self class]];
  #endif

    // load parameters from file 'world.setup'
    [ObjectLoader load: obj fromFileNamed: "world.setup"];

  return obj;
```

```
}

-createEnd
{
  return [super createEnd];
}

-(void)drop
{
  //drop all sub-objects
  [payoffs drop];
  [[allAgents getCollection] deleteAll];
  [[allAgents getCollection] drop];
  [allAgents drop];
  [populationDisplay drop];
  [worldDisplay drop];
  [world drop];
  [modelStep drop];
  [modelSchedule drop];

  [super drop];
}

-buildObjects
{
  id <List> tempList;
  id GamePayoffs;

  //load payoffs from file
  GamePayoffs=[Payoffs create: [self getZone]];
  [ObjectLoader load: GamePayoffs fromFileNamed: "payoffs.setup"];

  //create payoff matrix for interactions (matrix preserved for compatibility... will
be removed in future version)
  payoffs=[Array create: [self getZone] setCount: 2];
  [payoffs atOffset: 0 put: [Array create: [self getZone] setCount: 2]];
  [payoffs  atOffset: 1 put: [Array create: [self getZone] setCount: 2]];
  [[payoffs atOffset: 0] atOffset: 0 put: (id)[GamePayoffs getBBPayoff]];
  [[payoffs atOffset: 0] atOffset: 1 put: (id)[GamePayoffs getBAPayoff]];
  [[payoffs atOffset: 1] atOffset: 0 put: (id)[GamePayoffs getABPayoff]];
  [[payoffs atOffset: 1] atOffset: 1 put: (id)[GamePayoffs getAAPayoff]];

  //create global agent list
  tempList=[List create: [self getZone]];
  allAgents=[tempList begin: [tempList getZone]];

  //create lattice to store population density values for display
  populationDisplay=[Discrete2d createBegin: globalZone];
  [populationDisplay setSizeX: worldXsize Y: worldYsize];
  populationDisplay=[populationDisplay createEnd];
  [populationDisplay fillWithValue: 1];

  //create lattice to store cooperation and relatedness values for display
  worldDisplay=[Discrete2d createBegin: globalZone];
  [worldDisplay setSizeX: worldXsize Y: worldYsize];
  worldDisplay=[worldDisplay createEnd];
  [worldDisplay fillWithValue: 1];

  //create and initialise world
  world=[EPDWorld createBegin: globalZone];
  [world setSizeX: worldXsize Y: worldYsize];
  [world setupMaxAgents: maxAgents maxLocalAgents: maxLocalAgents startAgents:
startAgents strategyLength: strategyLength deathProbability: deathProbability
moveProbability: moveProbability mutationRate: mutationRate crossProbability:
crossProbability agentList: allAgents payoffMatrix: payoffs worldDisplay: worldDisplay
populationDisplay: populationDisplay startEnergy: startEnergy livingCost: livingCost];
  world=[world createEnd];

  //populate world with initial agent population
  [world populate];

  return self;
}

-buildActions
{
  //create action group to run model
```

```
  modelStep=[ActionGroup create: [self getZone]];
  [modelStep createActionForEach: [allAgents getCollection] message: M(move)];
  [modelStep createActionTo: world message: M(purge)];
  [modelStep createActionTo: world message: M(resetCoopLevel)];
  [modelStep createActionTo: world message: M(resetGlobalRelatedness)];
  [modelStep createActionTo: world message: M(resetCellTotalActions)];
  [modelStep createActionTo: world message: M(resetCellTotalDiversity)];
  [modelStep createActionTo: world message: M(resetDisplay)];
  [modelStep createActionTo: world message: M(updateAverageLocalPopSize)];
  [modelStep createActionForEach: [allAgents getCollection] message: M(play)];
//  [modelStep createActionForEach: [allAgents getCollection] message: M(mate)];
  [modelStep createActionTo: world message: M(mate)];
  [modelStep createActionTo: world message: M(display)];
  #ifdef observer
  #else
    [modelStep createActionTo: world message: M(storeValues)];
    [modelStep createActionTo: self message: M(checkToStop)];
  #endif

  modelSchedule=[Schedule createBegin: [self getZone]];
  [modelSchedule setRepeatInterval: 1];
  [modelSchedule setKeepEmptyFlag: NO];
  modelSchedule=[modelSchedule createEnd];

  [modelSchedule at: 0 createAction: modelStep];

  return self;
}

-activateIn: (id) swarmContext
{
  [super activateIn: swarmContext];

  [modelSchedule activateIn: self];

  return [self getActivity];
}

-getPopulationDisplay
{
  //return lattice containing population density values
  return populationDisplay;
}

-getWorldDisplay
{
  //return lattice containing cooperation and relatedness values
  return worldDisplay;
}

-getWorld
{
  return world;
}

-(int)getWorldXSize
{
  return (int)worldXsize;
}

-(int)getWorldYSize
{
  return (int)worldYsize;
}

-setMoveProbability: (double) moveProb
{
  //set agents' movement probability
  moveProbability=moveProb;

  return self;
}

-checkToStop
{
  //check if model run should end
  if ([world getWorldTime]==endTime || [world getWorldPopulation]==0)
```

```
  {
    [[self getActivity] terminate];
  }

  //if run has not ended, increment world's age
  [world incrementWorldTime];

  return self;
}

@end
```

EPDAgent.h

```
//EPDAgent.h EPD

#import <objectbase/SwarmObject.h>
#import <collections.h>
#import "EPDDefines.h"
#import "EPDWorld.h"
#import "DoubleData.h"
#import <random.h>

@interface EPDAgent: SwarmObject
{
  BOOL alive;
  BOOL played;
  BOOL mated;
  id strategy;
//  id <ListIndex> history;
  id history;
  int x, y, currentAction;
  float fitness;
  int totalInteractions, totalFitness;
  int energy;
  id myWorld;
}

-setupWorld: world x: (int) xPos y: (int) yPos;

-createEnd;

-move;
-play;
-mate;
-(float)getFitness;
-(id)getHistory;
-(id)getStrategy;
-(void)setStrategyAtOffset: (int) offset value: (int) value;
-(BOOL)isAlive;
-(BOOL)hasPlayed;
-(BOOL)hasMated;
-(void)setMated;
-(int)getCurrentAction;
-(void)setCurrentAction: (int) action;
-(void)updateFitness: (int) payoff;
-(void)increaseEnergy: (int) payoff;
-(void)drop;

@end
```

EPDAgent.m

```
//EPDAgent.m EPD

#import "EPDAgent.h"

@implementation EPDAgent

-setupWorld: world x: (int) xStart y: (int) yStart
{
  //initialise agent with information on the world they inhabit, their position within
it, and their state
  id <List> tempList;
```

```
  alive=YES; //the agent is alive
  played=NO; //the agent has not played the PD this round
  mated=NO; //the agent has not mated this round
  myWorld=world; //the world the agent inhabits
  //create the agent's strategy chromosome
  strategy=[Array create: [self getZone] setCount: [world getStrategyLength]];
  //create the agent's history (memory of previous PD interactions with other agents
  tempList=[List create: [self getZone]];
  history=[tempList begin: [tempList getZone]];
  x=xStart; //the agent's x-coordinate in the world
  y=yStart; //the agent's y-coordinate in the world
  fitness=0;
  totalInteractions=0; //the total number of PD interactions the agent has had
  totalFitness=0; //the total payoffs resulting from PD interactions the agent has had
  energy=[myWorld getStartEnergy]; //the agent's energy level
  return self;
}

-createEnd
{
  return [super createEnd];
}

-move
{
  id <ListIndex> myList;
  int l, xChange, yChange;

  if ([uniformDblRand getDoubleWithMin: 0 withMax: 1]>[myWorld getDeathProbability] &&
energy>0)
  {
    //the agent has sufficient energy and has not died through 'natural causes'... the
agent lives
    played=NO;
    mated=NO;
    energy=energy-[myWorld getLivingCost]; //decrease agent's energy level
    if ([uniformDblRand getDoubleWithMin: 0 withMax: 1]<[myWorld getMoveProbability])
//agent moves with certain probability
    {
      //agent moves
      //remove agent from current local cell list in world
      myList=[myWorld getObjectAtX: x Y: y];
      [myList setLoc: Start];
      if ([myList findNext: self])
      {
        [myList remove];
      }
      else
      {
        printf("Unable to remove agent from list\n");
      }

      //randomly determine neighbouring cell to move into
      xChange=0;
      yChange=0;
      while (xChange==0 && yChange==0)
      {
        xChange=[uniformIntRand getIntegerWithMin: -1 withMax: 1];
        yChange=[uniformIntRand getIntegerWithMin: -1 withMax: 1];
      }
      x=x+xChange;
      y=y+yChange;
      x=(x+[myWorld getSizeX])%[myWorld getSizeX];
      y=(y+[myWorld getSizeY])%[myWorld getSizeY];

      //add agent to new local cell list in world
      myList=[myWorld getObjectAtX: x Y: y];
      [[myList getCollection] addFirst: self];
    }
  }
  else
  {
    //agent dies

    alive=NO;
```

```
    //decrease frequency of agent's alleles in gene pool
    for (l=0; l<[myWorld getStrategyLength]; l++)
    {
      if ((int)[[self getStrategy] atOffset: l]==1)
      {
        [myWorld decreaseAlleleFrequency: l];
      }
    }

    //remove agent from local cell list in world
    myList=[myWorld getObjectAtX: x Y: y];
    [myList setLoc: Start];
    if ([myList findNext: self])
    {
      [myList remove];
    }
    else
    {
      printf("Couldn't find agent on local list\n");
    }
  }

  return self;
}

-play
{
  int agentsHere;
  int agentToPlayWith;
  int myPreviousChoice, theirPreviousChoice;
  int myCurrentChoice, theirCurrentChoice;
  int myPayoff, theirPayoff;
  int interactionLength;
  id historyItem1, historyItem2, potentialPartner, partner, localList;
#ifdef relatedness_measure3
  int l1;
  id alleles;
  double diversity;
#endif
#ifdef interaction_method2
  int l2;
#endif

  //here to prevent compiler warnings
  myCurrentChoice=0;
  theirCurrentChoice=0;
  myPreviousChoice=0;
  theirPreviousChoice=0;
  historyItem1=nil;
  historyItem2=nil;
  partner=nil;
  interactionLength=0;

  //find how many potential free partners are here from the agent's local cell list
  agentsHere=0;
  localList=[myWorld getObjectAtX: x Y: y];
  [localList setLoc: Start];
  if (played==NO)
  {
    while ((potentialPartner=[localList next]))
    {
      if (potentialPartner!=self && [potentialPartner hasPlayed]==NO) //check if this
partner is not the agent, and if they haven't played the PD this round
      {
        agentsHere++; //this is a valid partner
      }
    }
  }
  //if there are other free partners here, pick one at random to play against
  if (agentsHere>0)
  {
    agentToPlayWith=[uniformIntRand getIntegerWithMin: 0 withMax: agentsHere-1];
//randomly select a partner
    [localList setLoc: Start];
    //find that partner in the local cell list
    while ((potentialPartner=[localList next]))
    {
```

```
      if (potentialPartner!=self && [potentialPartner hasPlayed]==NO)
      {
        if (agentToPlayWith==0)
        {
          partner=potentialPartner;
        }
        else
        {
          agentToPlayWith--;
        }
      }
    }

    #ifdef relatedness_measure3
      //calculate the interacting agent's allelic diversity
      alleles=[Array create: [self getZone] setCount: [myWorld getStrategyLength]];
      diversity=0;
      #ifdef relatedness_measure4
        for (l1=2; l1<4; l1++)
        {
          [alleles atOffset: l1 put: [DoubleData create: [self getZone]]];
          [[alleles atOffset: l1] setDoubleData: (double)((int)[strategy atOffset:
l1]+(int)[[partner getStrategy] atOffset: l1])/2];
          diversity=diversity+1-(4*((0.5-[[alleles atOffset: l1] getDoubleData])*(0.5-
[[alleles atOffset: l1] getDoubleData])));
        }
        diversity=diversity/2;
      #else
        for (l1=0; l1<[myWorld getStrategyLength]; l1++)
        {
          [alleles atOffset: l1 put: [DoubleData create: [self getZone]]];
          [[alleles atOffset: l1] setDoubleData: (double)((int)[strategy atOffset:
l1]+(int)[[partner getStrategy] atOffset: l1])/2];
          diversity=diversity+1-(4*((0.5-[[alleles atOffset: l1] getDoubleData])*(0.5-
[[alleles atOffset: l1] getDoubleData])));
        }
        diversity=diversity/[myWorld getStrategyLength];
      #endif
    #endif

    #ifdef interaction_method2
      //repeat PD interaction for 3 iterations
      for (l2=0; l2<3; l2++)
      {
    #endif
    #ifdef pure_kin_selection
      //randomly assign roles between agents (used by each agent to choose which
strategy locus to use in this interaction)
      if ([uniformDblRand getDoubleWithMin: 0 withMax: 1]<0.5)
      {
        myCurrentChoice=(int)[strategy atOffset: 0];
        theirCurrentChoice=(int)[[partner getStrategy] atOffset: 1];
      }
      else
      {
        myCurrentChoice=(int)[strategy atOffset: 1];
        theirCurrentChoice=(int)[[partner getStrategy] atOffset: 0];
      }
    #else
      //see if the agent has played this partner before by checking the agent's
interaction history
      myPreviousChoice=-1;
      theirPreviousChoice=-1;
      interactionLength=0;
      [history setLoc: Start];
      [[partner getHistory] setLoc: Start];
      while ((historyItem1=[history next]) && [historyItem1 atOffset: 0]!=partner)
      {
      }
      if ([historyItem1 atOffset: 0]==partner)
      {
        //this partner has been played before, recover the actions from the last
interaction
        myPreviousChoice=(int)[historyItem1 atOffset: 1];
        theirPreviousChoice=(int)[historyItem1 atOffset: 2];
        interactionLength=(int)[historyItem1 atOffset: 3];
        //find partner's memory of last interaction
```

```
        while ((historyItem2=[[partner getHistory] next]) && [historyItem2 atOffset:
0]!=self)
        {
        }
      }
      if (myPreviousChoice!=-1 && theirPreviousChoice!=-1)
      {
        //these agents have played before
        if (myPreviousChoice==0 && theirPreviousChoice==0)
        {
          //last time the agent played B and their partner played B
          myCurrentChoice=(int)[strategy atOffset: 4];
          theirCurrentChoice=(int)[[partner getStrategy] atOffset: 4];
        }
        if (myPreviousChoice==0 && theirPreviousChoice==1)
        {
          //last time the agent played B and their partner played A
          myCurrentChoice=(int)[strategy atOffset: 2];
          theirCurrentChoice=(int)[[partner getStrategy] atOffset: 3];
        }
        if (myPreviousChoice==1 && theirPreviousChoice==1)
        {
          //last time the agent played A and their partner played A
          myCurrentChoice=(int)[strategy atOffset: 1];
          theirCurrentChoice=(int)[[partner getStrategy] atOffset: 1];
        }
        if (myPreviousChoice==1 && theirPreviousChoice==0)
        {
          //last time the agent played A and their partner played B
          myCurrentChoice=(int)[strategy atOffset: 3];
          theirCurrentChoice=(int)[[partner getStrategy] atOffset: 2];
        }
      }
      else
      {
        //these agents have never met before
        myCurrentChoice=(int)[strategy atOffset: 0];
        theirCurrentChoice=(int)[[partner getStrategy] atOffset: 0];
        historyItem1=[Array create: [self getZone] setCount: 4];
        [[history getCollection] addFirst: historyItem1];
        historyItem2=[Array create: [self getZone] setCount: 4];
        [[[partner getHistory] getCollection] addFirst: historyItem2];
      }
      //add this interaction to my history
      interactionLength++;
      [historyItem1 atOffset: 0 put: partner];
      [historyItem1 atOffset: 1 put: (id)myCurrentChoice];
      [historyItem1 atOffset: 2 put: (id)theirCurrentChoice];
      [historyItem1 atOffset: 3 put: (id)interactionLength];
      //add this interaction to their history
      [historyItem2 atOffset: 0 put: self];
      [historyItem2 atOffset: 1 put: (id)theirCurrentChoice];
      [historyItem2 atOffset: 2 put: (id)myCurrentChoice];
      [historyItem2 atOffset: 3 put: (id)interactionLength];
    #endif
    //update fitnesses
    myPayoff=[myWorld getPayoffAction1: myCurrentChoice action2: theirCurrentChoice];
    theirPayoff=[myWorld getPayoffAction1: theirCurrentChoice action2:
myCurrentChoice];
    [self updateFitness: myPayoff];
    [partner updateFitness: theirPayoff];
    //update energy levels
    [self increaseEnergy: myPayoff];
    [partner increaseEnergy: theirPayoff];
    //update cooperation level
    #ifdef consider_interaction_subset
      if ((myPreviousChoice==0 && theirPreviousChoice==1) || (myPreviousChoice==1 &&
theirPreviousChoice==0))
      {
    #endif
        #ifdef role_swap_cooperation
          if ((myCurrentChoice==0 && theirCurrentChoice==1) || (myCurrentChoice==1 &&
theirCurrentChoice==0))
          {
            [myWorld updateCoopLevelMyAction: 1 TheirAction: 1];
            [myWorld incrementTotalCooperativeActionsAtX: x Y: y NumCoopActions: 2];
          }
```

```
          else
          {
            [myWorld updateCoopLevelMyAction: 0 TheirAction: 0];
          }
          [myWorld incrementTotalActionsAtX: x Y: y NumActions: 2];
        #else
          [myWorld updateCoopLevelMyAction: myCurrentChoice TheirAction:
theirCurrentChoice];
          [myWorld incrementTotalCooperativeActionsAtX: x Y: y NumCoopActions:
myCurrentChoice+theirCurrentChoice];
          [myWorld incrementTotalActionsAtX: x Y: y NumActions: 2];
        #endif
    #ifdef consider_interaction_subset
      }
    #endif
    //set agents' current action
    currentAction=myCurrentChoice;
    [partner setCurrentAction: theirCurrentChoice];

    #ifdef relatedness_measure3
      #ifdef consider_interaction_subset
        if ((myPreviousChoice==0 && theirPreviousChoice==1) || (myPreviousChoice==1 &&
theirPreviousChoice==0))
        {
      #endif
          [myWorld increaseGlobalRelatedness: 1-diversity];
          [myWorld incrementTotalDiversityAtX: x Y: y Diversity: diversity];
      #ifdef consider_interaction_subset
        }
      #endif
    #endif
    #ifdef interaction_method2
      } //terminate for loop for iterated PD interaction
    #endif

    #ifdef relatedness_measure3
      //drop the allele frequency array
      for (l1=0; l1<[myWorld getStrategyLength]; l1++)
      {
        [[alleles atOffset: l1] drop];
      }
      [alleles drop];
    #endif
  }

  return self;
}

-mate
{
  int agentsHere, agentToMateWith;
  int l1;
#ifdef global_mating_pool
  int newX, newY;
#endif
  id potentialPartner, partner, matingList, newAgent, mainParent, otherParent;

  //here to prevent compiler warning
  partner=nil;

  //find how many potential free partners are here from the agent's local cell list
  agentsHere=0;
#ifdef global_mating_pool
  matingList=[myWorld getAllAgents];
#else
  matingList=[myWorld getObjectAtX: x Y: y];
#endif
  [matingList setLoc: Start];
#ifdef global_population_regulation
  if (mated==NO && [uniformDblRand getDoubleWithMin: 0 withMax: 1]<1-((double)[myWorld
getWorldPopulation]/(double)[myWorld getMaxAgents])) //agent can mate if it hasn't
already done so, and with a probability inversely proportional to the global
population size
#else
  if (mated==NO && [uniformDblRand getDoubleWithMin: 0 withMax: 1]<1-
((double)[[matingList getCollection] getCount]/(double)[myWorld getMaxLocalAgents]))
```

```
//agent can mate if it hasn't already done so, and with a probability inversely
proportional to the local population size
#endif
  {
    while ((potentialPartner=[matingList next]))
    {
      if (potentialPartner!=self && [potentialPartner hasMated]==NO) //check if this
partner is not the agent, and if they have not already mated
      {
        agentsHere++;
      }
    }
  }
  //if there are other free partners here, pick one at random to mate with
  if (agentsHere>0)
  {
    agentToMateWith=[uniformIntRand getIntegerWithMin: 0 withMax: agentsHere-1];
//randomly select a partner
    [matingList setLoc: Start];
    while ((potentialPartner=[matingList next]))
    {
      if (potentialPartner!=self && [potentialPartner hasMated]==NO)
      {
        if (agentToMateWith==0)
        {
          partner=potentialPartner;
        }
        else
        {
          agentToMateWith--;
        }
      }
    }

    //set agent and partner as mated
    [self setMated];
    [partner setMated];

    //create an offspring agent
    newAgent=[EPDAgent createBegin: [self getZone]];
#ifdef global_mating_pool
    newX=[uniformIntRand getIntegerWithMin: 0 withMax: [myWorld getSizeX]-1];
    newY=[uniformIntRand getIntegerWithMin: 0 withMax: [myWorld getSizeY]-1];
    [newAgent setupWorld: myWorld x: newX y: newY];
#else
    [newAgent setupWorld: myWorld x: x y: y];
#endif
    newAgent=[newAgent createEnd];
    //set offspring as mated so no other agents mate with it during this time step
    [newAgent setMated];
    //initialise offspring agent's chromosome with parameterised crossover and
mutation
    //choose main parent with 50% probability (avoids bias in transmission of parental
genetic material)
    if ([uniformDblRand getDoubleWithMin: 0 withMax: 1]<0.5)
    {
      mainParent=self;
      otherParent=partner;
    }
    else
    {
      mainParent=partner;
      otherParent=self;
    }
    //combine parental genetic material with parameterised crossover operator
    for (l1=0; l1<[myWorld getStrategyLength]; l1++)
    {
      if ([uniformDblRand getDoubleWithMin: 0 withMax: 1]<[myWorld
getCrossProbability])
      {
        //allele taken from other parent
        [newAgent setStrategyAtOffset: l1 value: (int) [[otherParent getStrategy]
atOffset: l1]];
      }
      else
      {
        //allele taken from main parent
```

```
        [newAgent setStrategyAtOffset: l1 value: (int) [[mainParent getStrategy]
atOffset: l1]];
      }
      //apply mutation operator
      if ([uniformDblRand getDoubleWithMin: 0 withMax: 1]<[myWorld getMutationRate])
      {
        //allele mutates
        [newAgent setStrategyAtOffset: l1 value: (int) 1-(int)[[newAgent getStrategy]
atOffset: l1]];
      }
      //update frequency of allele in gene pool
      if ((int)[[newAgent getStrategy] atOffset: l1]==1)
      {
        [myWorld increaseAlleleFrequency: l1];
      }
    }
  #ifdef global_mating_pool
    [[[myWorld getObjectAtX: newX Y: newY] getCollection] addLast: newAgent]; //add
offspring agent to random cell list
  #else
    [[matingList getCollection] addLast: newAgent]; //add offspring agent to local
cell list
  #endif
    [myWorld addAgent: newAgent]; //add offspring agent to global agent list
  }

  return self;
}

-(float)getFitness
{
  //return agent's fitness level
  return fitness;
}

-(id)getHistory
{
  //return agent's interaction history
  return history;
}

-(id)getStrategy
{
  //return agent's strategy chromosome
  return strategy;
}

-(void) setStrategyAtOffset: (int) offset value: (int) value
{
  //set allele at locus on agent's strategy chromosome
  [strategy atOffset: offset put: (id)value];
}

-(BOOL)isAlive
{
  //return the agent's status (YES=alive, NO=dead)
  return alive;
}

-(BOOL)hasPlayed
{
  //return the agent's play status (YES=has played this round, NO=has not played)
  return played;
}

-(BOOL)hasMated
{
  //return the agent's mating status (YES=has mated this round, NO=has not mated)
  return mated;
}

-(void)setMated
{
  //set the agent's status to indicate it has mated this round
  mated=YES;
}
```

```
-(int)getCurrentAction
{
  //return the agent's action (C or D) for this round
  return currentAction;
}

-(void)setCurrentAction: (int) action
{
  //set the agent's current action (C or D) for this round
  currentAction=action;
}

-(void)updateFitness: (int) payoff
{
  //update the agent's fitness level according to payoff received from PD interaction
  totalInteractions++;
  totalFitness=totalFitness+payoff;
  fitness=totalFitness/totalInteractions;
  played=YES; //set the agent's status to indicate it has played this round
}

-(void)increaseEnergy: (int) payoff
{
  //increase the agent's energy level
  energy=energy+payoff;
}

-(void)drop
{
  //destroy the agent object
  [strategy drop]; //drop the agent's strategy chromosome
  //delete the contents of the agent's interaction history
  [[history getCollection] deleteAll];
  [[history getCollection] drop];
  [history drop]; //drop the agent's interaction history

  [super drop];
}

@end
```

EPDWorld.h

```
//EPDWorld.h EPD

#import <space.h>
#import <collections.h>
#import <random.h>
#import <objectbase/SwarmObject.h>
#import <analysis.h>
#import <space/Discrete2d.h>
#import "EPDDefines.h"
#import "IntegerData.h"
#import "DoubleData.h"

//#define debug

@interface EPDWorld : Discrete2d
{
  int maxAgents, maxLocalAgents, startAgents, strategyLength, cooperativeActions,
totalActions;
  int totalInteractions, totalInteractionLength;
  int totalPartners, totalInteractants;
  int totalPopulationSize, totalPopulatedCells;
  int startEnergy, livingCost, worldTime;
  float mutationRate, crossProbability;
  double deathProbability, moveProbability, cooperationLevel, globalRelatedness;
//  id <ListIndex> allAgents;
  id allAgents;
  id <Array> alleleFrequencies;
  id payoffs;
  id worldDisplay, populationDisplay;
  id cellTotalDiversity, cellDiversityDivisor, cellTotalCooperativeActions,
cellTotalActions;
//  id <ListIndex> cooperationValues;
```

```
  id cooperationValues;
//  id <ListIndex> relatednessValues;
  id relatednessValues;
}

-setupMaxAgents: (int) maxPop maxLocalAgents: (int) maxLocalPop startAgents: (int)
startPop strategyLength: (int) stratLen deathProbability: (double) deathProb
moveProbability: (double) moveProb mutationRate: (float) mu crossProbability: (float)
crossProb agentList: aListIndex payoffMatrix: anArray worldDisplay: aDisplay
populationDisplay: bDisplay startEnergy: (int) startEnergy livingCost: (int)
livingCost;

-createEnd;
-(void)drop;

-populate;
-addAgent: newAgent;
-purge;
-mate;
-display;
-(int)getMaxAgents;
-(int)getMaxLocalAgents;
-(int)getWorldPopulation;
-getAllAgents;
-(int)getGlobalRelatedness;
-increaseGlobalRelatedness: (double) increase;
-resetGlobalRelatedness;
-(int)getStrategyLength;
-(double)getDeathProbability;
-(double)getMoveProbability;
-(float)getMutationRate;
-(float)getCrossProbability;
-(int)getPayoffAction1: (int) action1 action2: (int) action2;
-resetCoopLevel;
-(int)getCoopLevel;
-increaseAlleleFrequency: (int) alleleNum;
-decreaseAlleleFrequency: (int) alleleNum;
-getAlleleFrequency: (int) alleleNum;
-updateCoopLevelMyAction: (int) action1 TheirAction: (int) action2;
-(int)getStartEnergy;
-(int)getLivingCost;
-(int)getWorldTime;
-incrementWorldTime;
-storeValues;
-(int)getAverageCooperationLevel;
-(double)getAverageNumberOfPartners;
-(int)getAverageRelatedness;
-(double)getAverageInteractionLength;
-updateAverageLocalPopSize;
-(double)getAverageLocalPopSize;
-getWorldDisplay;
-resetDisplay;
-incrementTotalActionsAtX: (int) x Y: (int) y NumActions: (int) numActions;
-incrementTotalCooperativeActionsAtX: (int) x Y: (int) y NumCoopActions: (int)
numCoopActions;
-incrementTotalDiversityAtX: (int) x Y: (int) y Diversity: (double) diversity;
-(double)getCooperationLevelAtX: (int) x Y: (int) y;
-(double)getDiversityLevelAtX: (int) x Y: (int) y;
-resetCellTotalActions;
-resetCellTotalDiversity;
@end
```

EPDWorld.m

```
//EPDWorld.m EPD

#import "EPDWorld.h"
#import "EPDAgent.h"

@implementation EPDWorld

-setupMaxAgents: (int) maxPop maxLocalAgents: (int) maxLocalPop startAgents: (int)
startPop strategyLength: (int) stratLen deathProbability: (double) deathProb
moveProbability: (double) moveProb mutationRate: (float) mu crossProbability: (float)
```

```
crossProb agentList: aListIndex payoffMatrix: anArray worldDisplay: aDisplay
populationDisplay: bDisplay startEnergy: (int) energy livingCost: (int) cost
{
  //initialise the world parameters and objects
  int l;
  id tempList;
  worldTime=0;
  maxAgents=maxPop;
  maxLocalAgents=maxLocalPop;
  startAgents=startPop;
  strategyLength=stratLen;
  deathProbability=deathProb;
  moveProbability=moveProb;
  mutationRate=mu;
  crossProbability=crossProb;
  startEnergy=energy;
  livingCost=cost;
  allAgents=aListIndex;
  payoffs=anArray;
  worldDisplay=aDisplay;
  populationDisplay=bDisplay;
  totalActions=0;
  cooperationLevel=0;
  totalInteractions=0;
  totalInteractionLength=0;
  totalPartners=0;
  totalInteractants=0;
  totalPopulationSize=0;
  totalPopulatedCells=0;
  //create the allele frequency array
  alleleFrequencies=[Array create: [self getZone] setCount: strategyLength];
  for (l=0; l<strategyLength; l++)
  {
    [alleleFrequencies atOffset: l put: [IntegerData create: [self getZone]]];
  }
  //create the cooperation and relatedness level histories
  tempList=[List create: [self getZone]];
  cooperationValues=[tempList begin: [tempList getZone]];
  tempList=[List create: [self getZone]];
  relatednessValues=[tempList begin: [tempList getZone]];

  //create the lattice to store the total diversity of cells
  cellTotalDiversity=[Discrete2d createBegin: globalZone];
  [cellTotalDiversity setSizeX: [self getSizeX] Y: [self getSizeY]];
  cellTotalDiversity=[cellTotalDiversity createEnd];
  [cellTotalDiversity fillWithValue: 0];
  //create the lattice to store the total diversity of cells
  cellDiversityDivisor=[Discrete2d createBegin: globalZone];
  [cellDiversityDivisor setSizeX: [self getSizeX] Y: [self getSizeY]];
  cellDiversityDivisor=[cellDiversityDivisor createEnd];
  [cellDiversityDivisor fillWithValue: 0];
  //create the lattice to store the total diversity of cells
  cellTotalCooperativeActions=[Discrete2d createBegin: globalZone];
  [cellTotalCooperativeActions setSizeX: [self getSizeX] Y: [self getSizeY]];
  cellTotalCooperativeActions=[cellTotalCooperativeActions createEnd];
  [cellTotalCooperativeActions fillWithValue: 0];
  //create the lattice to store the total diversity of cells
  cellTotalActions=[Discrete2d createBegin: globalZone];
  [cellTotalActions setSizeX: [self getSizeX] Y: [self getSizeY]];
  cellTotalActions=[cellTotalActions createEnd];
  [cellTotalActions fillWithValue: 0];

  return self;
}

-createEnd
{
  return [super createEnd];
}

-(void)drop
{
  int x,y;

  //drop the allele frequency array
  [alleleFrequencies drop];
  //drop the cooperation and relatedness level histories
```

```
  [[cooperationValues getCollection] deleteAll];
  [[cooperationValues getCollection] drop];
  [cooperationValues drop];
  [[relatednessValues getCollection] deleteAll];
  [[relatednessValues getCollection] drop];
  [relatednessValues drop];
  //drop the local cell lists
  for (x=0; x<xsize; x++)
  {
    for (y=0; y<ysize; y++)
    {
      [[[self getObjectAtX: x Y: y] getCollection] drop];
      [[self getObjectAtX: x Y: y] drop];
    }
  }
  [cellTotalDiversity drop];
  [cellDiversityDivisor drop];
  [cellTotalCooperativeActions drop];
  [cellTotalActions drop];

  [super drop];
}

-populate
{
  int l1,l2,x,y;
  id newAgent;
  id <List> tempList;
//  id <ListIndex> localList;
  id localList;

  //create the local cell lists
  for (x=0; x<xsize; x++)
  {
    for (y=0; y<ysize; y++)
    {
      tempList=[List create: [self getZone]];
      localList=[tempList begin: [tempList getZone]];
      [self putObject: localList atX: x Y: y];
    }
  }
  //create the initial agent population
  for (l1=0; l1<startAgents; l1++)
  {
    //randomly place agent in environment
    x=[uniformIntRand getIntegerWithMin: 0 withMax: xsize-1];
    y=[uniformIntRand getIntegerWithMin: 0 withMax: ysize-1];
    //create new agent
    newAgent=[EPDAgent createBegin: [self getZone]];
    [newAgent setupWorld: self x: x y: y];
    newAgent=[newAgent createEnd];
    //randomly initialise agent's strategy chromosome
    for (l2=0; l2<strategyLength; l2++)
    {
      [newAgent setStrategyAtOffset: l2 value: [uniformIntRand getIntegerWithMin: 0
withMax: 1]];
      if ((int)[[newAgent getStrategy] atOffset: l2]==1)
      {
        [self increaseAlleleFrequency: l2];
      }
    }
    [[[self getObjectAtX: x Y: y] getCollection] addFirst: newAgent];
    [[allAgents getCollection] addFirst: newAgent];
  }

  return self;
}

-addAgent: newAgent
{
  //add a new agent to the global list
  [[allAgents getCollection] addLast: newAgent];

  return self;
}

-purge
```

```
{
  id dyingAgent, forgettingAgent, historyItem;

  //remove agents who have died this step from the environment
  [allAgents setLoc: Start];
  while ((dyingAgent=[allAgents next]))
  {
    if ([dyingAgent isAlive]==NO) //check if this agent is dead
    {
      //store agent's interaction length statistics
      totalInteractants++;
      [[dyingAgent getHistory] setLoc: Start];
      while ((historyItem=[[dyingAgent getHistory] next]))
      {
        totalInteractions++;
        totalInteractionLength+=(int)[historyItem atOffset: 3];
        totalPartners++;
      }

      //remove histories involving the agent from the other agents' memories
      [allAgents setLoc: Start];
      while ((forgettingAgent=[allAgents next]))
      {
        [[forgettingAgent getHistory] setLoc: Start];
        while ((historyItem=[[forgettingAgent getHistory] next]))
        {
          if ([historyItem atOffset: 0]==dyingAgent)
          {
            [[forgettingAgent getHistory] remove];
            [historyItem drop];
          }
        }
      }

      [allAgents setLoc: Start];
      [allAgents findNext: dyingAgent];
      //remove the agent from the global list
      dyingAgent=[allAgents remove];
      [dyingAgent drop];
    }
  }

  return self;
}

-mate
{
  //randomise order of mating opportunities in global agent list
  int l1, l2, population, agentNumber, numAgentsMated;
  id agent, agentsMated;

  population=[self getWorldPopulation];
  if (population>0)
  {
    //create temporary array to remember if agents have had their mating opportunity
(represented by '1')
    agentsMated=[Array create: [self getZone] setCount: population];
    for (l1=0; l1<population; l1++)
    {
      [agentsMated atOffset: l1 put:(id)0];
    }

    numAgentsMated=0;
    for (l1=0; l1<population; l1++) //repeat for every agent in the population
    {
      //randomly choose an agent which hasn't had its mating opportunity
/* the old inefficient way of choosing
      agentNumber=[uniformIntRand getIntegerWithMin: 0 withMax: population-1];
      while ((int)[agentsMated atOffset: agentNumber]==1)
      {
        agentNumber=[uniformIntRand getIntegerWithMin: 0 withMax: population-1];
      }
      [agentsMated atOffset: agentNumber put:(id)1]; //flag the agent as having had
its mating opportunity
      //retrieve the agent from the global list
      [allAgents setLoc: Start];
      agent=[allAgents get]; // here to prevent compiler warning
```

```
      for (l2=0; l2<=agentNumber; l2++)
      {
        agent=[allAgents next];
      }

      [agent mate];
*/
      if (population-numAgentsMated>0)
      {
        agentNumber=[uniformIntRand getIntegerWithMin: 0 withMax: (population-
numAgentsMated)-1];
        [allAgents setLoc: Start];
        agent=[allAgents get]; // here to prevent compiler warning
        l2=0;
        while (agentNumber>=0)
        {
          agent=[allAgents next];
          if ((int)[agentsMated atOffset: l2]!=1)
          {
            agentNumber--;
          }
          if (agentNumber>=0)
          {
            l2++;
          }
        }
        [agentsMated atOffset: l2 put:(id)1]; //flag the agent as having had its
mating opportunity
        [agent mate]; //allow the agent to mate
        numAgentsMated++;
      }
    }
    [agentsMated drop];
  }

  return self;
}

-display
{
  id alleles;
  int x, y, l1, localPopulation;
#ifndef relatedness_measure3
  id agent;
#endif
#ifdef relatedness_measure2
  int populatedCells;
#endif
  double diversity;
  localPopulation=0;
  //create a temporary array used in calculating relatedness within a cell
  alleles=[Array create: [self getZone] setCount: strategyLength];
  for (l1=0; l1<strategyLength; l1++)
  {
    [alleles atOffset: l1 put: [DoubleData create: [self getZone]]];
  }

  #ifdef relatedness_measure2
    //calculate local cooperation and relatedness levels for all cells inhabited by
agents
    populatedCells=0;
    globalRelatedness=0;
  #endif

  #ifdef relatedness_measure3
    for (x=0; x<xsize; x++)
    {
      for (y=0; y<ysize; y++)
      {
        if ([[[self getObjectAtX: x Y: y] getCollection] getCount]>0) //check if cell
is inhabited
        {
          localPopulation=[[[self getObjectAtX: x Y: y] getCollection] getCount];
          if ([[[self getObjectAtX: x Y: y] getCollection] getCount]==1)
          {
            //cell inhabited by only one agent, colour red
            [worldDisplay putValue: 122 atX: x Y: y];
```

```
          }
          else
          {
            diversity=[self getDiversityLevelAtX: x Y: y];
             //draw the cooperation and relatedness of this cell on the world display
            [worldDisplay putValue: (int)([self getCooperationLevelAtX: x Y:
y]*10)*11+(1-diversity)*10+1 atX: x Y: y];
          }
          //draw the population density of this cell on the population display
          [populationDisplay putValue:
(long)(((double)localPopulation/maxAgents)*10+1) atX: x Y: y];
        }
        else
        {
          //draw this cell as uninhabited on the population and world displays
          [populationDisplay putValue: 0 atX: x Y: y];
          [worldDisplay putValue: 0 atX: x Y: y];
        }
      }
    }
  #else
    for (x=0; x<xsize; x++)
    {
      for (y=0; y<ysize; y++)
      {
        if ([[[self getObjectAtX: x Y: y] getCollection] getCount]>0) //check if cell
is inhabited
        {
          localPopulation=0;
          [[self getObjectAtX: x Y: y] setLoc: Start];
          //count the frequency of each allele in all the agents in this cell, and the
percentage of cooperative actions
          for (l1=0; l1<strategyLength; l1++)
          {
            [[alleles atOffset: l1] setDoubleData: 0];
          }
          while ((agent=[[self getObjectAtX: x Y: y] next]))
          {
            localPopulation++;
            for (l1=0; l1<strategyLength; l1++)
            {
              [[alleles atOffset: l1] setDoubleData: [[alleles atOffset: l1]
getDoubleData]+(int)[[agent getStrategy] atOffset: l1]];
            }
          }
          //calculate the genetic diversity of the population in this cell
          diversity=0;
          for (l1=0; l1<strategyLength; l1++)
          {
            [[alleles atOffset: l1] setDoubleData: [[alleles atOffset: l1]
getDoubleData]/[[[self getObjectAtX: x Y: y] getCollection] getCount]];
            diversity=diversity+1-(4*((0.5-[[alleles atOffset: l1]
getDoubleData])*(0.5-[[alleles atOffset: l1] getDoubleData])));
          }
          diversity=diversity/strategyLength;
          //draw the population density of this cell on the population display
          [populationDisplay putValue:
(long)(((double)localPopulation/maxAgents)*10+1) atX: x Y: y];
          //draw the cooperation and relatedness levels of this cell on the world
display
          if (localPopulation==1)
          {
            //cell inhabited by only one agent, colour red
            [worldDisplay putValue: 122 atX: x Y: y];
          }
          else
          {
            //draw the cooperation and relatedness of this cell on the world display
            [worldDisplay putValue: (int)([self getCooperationLevelAtX: x Y:
y]*10)*11+(1-diversity)*10+1 atX: x Y: y];

            #ifdef relatedness_measure2
              //increment counter of number of cells inhabited by more than one agent
              populatedCells++;
              //add cell relatedness to global relatedness total
              globalRelatedness+=(1-diversity);
            #endif
```

```
          }
        }
        else
        {
          //draw this cell as uninhabited on the population and world displays
          [populationDisplay putValue: 0 atX: x Y: y];
          [worldDisplay putValue: 0 atX: x Y: y];
        }
      }
    }
  #endif

  //drop the allele frequency array
  for (l1=1; l1<strategyLength; l1++)
  {
    [[alleles atOffset: l1] drop];
  }
  [alleles drop];

  #ifdef relatedness_measure2
    //calculate global relatedness
    if (populatedCells>0)
    {
      globalRelatedness=globalRelatedness/(double)populatedCells;
      globalRelatedness=globalRelatedness*100;
    }
    else
    {
      globalRelatedness=0;
    }
  #endif

  return self;
}

-(int)getMaxAgents
{
  //return the maximum number of agents the world can support
  return maxAgents;
}

-(int)getMaxLocalAgents
{
  //return the maximum number of agents a single cell can support
  return maxLocalAgents;
}

-(int)getWorldPopulation
{
  //return the current world population
  return (int)[[allAgents getCollection] getCount];
}

-getAllAgents
{
  //return the world population list
  return allAgents;
}

-(int)getGlobalRelatedness
{
  //return the global relatedness of the agent population
  #ifdef relatedness_measure1
    id alleles, agent;
    int l1;
    double diversity;

    if ([self getWorldPopulation]>0)
    {
      //count frequencies of alleles in all agents in the world
      alleles=[Array create: [self getZone] setCount: strategyLength];
      for (l1=0; l1<strategyLength; l1++)
      {
        [alleles atOffset: l1 put: [DoubleData create: [self getZone]]];
        [[alleles atOffset: l1] setDoubleData: 0];
      }
      [allAgents setLoc: Start];
```

```
      while ((agent=[allAgents next]))
      {
        for (l1=0; l1<strategyLength; l1++)
        {
          [[alleles atOffset: l1] setDoubleData: [[alleles atOffset: l1]
getDoubleData]+(int)[[agent getStrategy] atOffset: l1]];
        }
      }
      //calculate genetic diversity of all agents in the world
      diversity=0;
      for (l1=0; l1<strategyLength; l1++)
      {
        [[alleles atOffset: l1] setDoubleData: [[alleles atOffset: l1]
getDoubleData]/[[allAgents getCollection] getCount]];
        diversity=diversity+1-(4*((0.5-[[alleles atOffset: l1] getDoubleData])*(0.5-
[[alleles atOffset: l1] getDoubleData])));
      }
      diversity=diversity/strategyLength;
      globalRelatedness=(1-diversity)*100;
      //drop allele frequency array
      for (l1=0; l1<strategyLength; l1++)
      {
        [[alleles atOffset: l1] drop];
      }
      [alleles drop];
    }
    else
    {
      globalRelatedness=0;
    }
    return (int)globalRelatedness;
  #endif

  #ifdef relatedness_measure2
    return (int)globalRelatedness;
  #endif

  #ifdef relatedness_measure3
    if (totalActions>0)
    {
      return (int)((globalRelatedness/(double)(totalActions/2))*100);
    }
    else
    {
      return 0;
    }
  #endif
}

-increaseGlobalRelatedness: (double) increase;
{
  globalRelatedness+=increase;

  return self;
}

-resetGlobalRelatedness
{
  globalRelatedness=0;

  return self;
}

-(int)getStrategyLength
{
  //return the length of agents' strategy chromosomes
  return strategyLength;
}

-(double)getDeathProbability
{
  //return the envorinmental probability of death
  return deathProbability;
}

-(double)getMoveProbability
{
```

```
  //return the agent movement probability
  return moveProbability;
}

-(float)getMutationRate
{
  //return the mutation rate
  return mutationRate;
}

-(float)getCrossProbability
{
  //return the parameterised crossover probability
  return crossProbability;
}

-(int)getPayoffAction1: (int) action1 action2: (int) action2;
{
  //return the PD payoff for an action pair
  return (int)[[payoffs atOffset: action1] atOffset: action2];
}

-resetCoopLevel;
{
  //reset the variables used in calculating the global cooperation level
  totalActions=0;
  cooperativeActions=0;

  return self;
}

-(int)getCoopLevel
{
  //return the global cooperation level
  if (totalActions>0)
  {
    cooperationLevel=(double)cooperativeActions/(double)totalActions;
  }
  else
  {
    cooperationLevel=0;
  }

  return (int)(cooperationLevel*100);
}

-increaseAlleleFrequency: (int) alleleNum
{
  //increase the frequency of an allele in the gene pool
  int t=[[alleleFrequencies atOffset: alleleNum] getIntData];
  [[alleleFrequencies atOffset: alleleNum] setIntData: t+1];

  return self;
}

-decreaseAlleleFrequency: (int) alleleNum
{
  //decrease the frequency of an allele in the gene pool
  int t=[[alleleFrequencies atOffset: alleleNum] getIntData];
  [[alleleFrequencies atOffset: alleleNum] setIntData: t-1];

  return self;
}

-getAlleleFrequency: (int) alleleNum
{
  //return the frequency of an allele in the gene pool
  return [alleleFrequencies atOffset: alleleNum];
}

-updateCoopLevelMyAction: (int) action1 TheirAction: (int) action2
{
  //update the variables used in calculating the global cooperation level
  totalActions=totalActions+2;
  cooperativeActions=cooperativeActions+action1+action2;

  return self;
```

```
}

-(int)getStartEnergy
{
  //return the initial energy level allocated to new agents
  return startEnergy;
}

-(int)getLivingCost
{
  //return the energy cost of living for each time step
  return livingCost;
}

-(int)getWorldTime
{
  //return the world's age
  return worldTime;
}

-incrementWorldTime
{
  //increment the world's age
  worldTime++;

  return self;
}

-storeValues
{
  //store the global cooperation and relatedness levels for this time step
  id coopValue, relValue;

  #ifdef consider_interaction_subset
    if (totalActions>0)
    {
  #endif
      coopValue=[IntegerData create: [self getZone]];
      [coopValue setIntData: (int)[self getCoopLevel]];
      [[cooperationValues getCollection] addLast: coopValue];
      relValue=[IntegerData create: [self getZone]];
      [relValue setIntData: (int)[self getGlobalRelatedness]];
      [[relatednessValues getCollection] addLast: relValue];
  #ifdef consider_interaction_subset
    }
  #endif

  return self;
}

-(int)getAverageCooperationLevel
{
  //return the average cooperation level over the world's history
  int total=0;
  id value;

  [cooperationValues setLoc: Start];
  while ((value=[cooperationValues next]))
  {
    total+=[value getIntData];
  }

  return (int)((double)total/(double)[[cooperationValues getCollection] getCount]);
}

-(double)getAverageNumberOfPartners
{
  // return average number of interaction partners per agent over the world's history
  return ((double)totalPartners/(double)totalInteractants);
}

-(int)getAverageRelatedness
{
  //return the average global relatedness over the world's history
  int total=0;
  id value;
```

```
  [relatednessValues setLoc: Start];
  while ((value=[relatednessValues next]))
  {
    total+=[value getIntData];
  }

  return (int)((double)total/(double)[[relatednessValues getCollection] getCount]);
}

-(double)getAverageInteractionLength
{
  //return the average length of iterated PD interactions in the world
  #ifdef pure_kin_selection
    return 0; //average interaction length not calculated for pure kin selection model
as not of interest
  #else
    return (double)totalInteractionLength/(double)totalInteractions;
  #endif
}

-updateAverageLocalPopSize
{
  //update the average cell population size in the world
  int x, y;

  totalPopulationSize+=[[allAgents getCollection] getCount];
  for (x=0; x<xsize; x++)
  {
    for (y=0; y<ysize; y++)
    {
      if ([[[self getObjectAtX: x Y: y] getCollection] getCount]>0)
      {
        totalPopulatedCells++;
      }
    }
  }

  return self;
}

-(double)getAverageLocalPopSize
{
  //return the average cell population size in the world
  return (double)totalPopulationSize/(double)totalPopulatedCells;
}

-getWorldDisplay
{
  //return the array used to draw the world display
  return worldDisplay;
}

-resetDisplay
{
  //reset the world display
  int x,y;
  for (x=0; x<xsize; x++)
  {
    for (y=0; y<ysize; y++)
    {
      [worldDisplay putValue: 0 atX: x Y: y];
    }
  }

  return self;
}

-incrementTotalActionsAtX: (int) x Y: (int) y NumActions: (int) numActions
{
  [cellTotalActions putValue: [cellTotalActions getValueAtX: x Y: y]+numActions atX: x
Y: y];

  return self;
}

-incrementTotalCooperativeActionsAtX: (int) x Y: (int) y NumCoopActions: (int)
numCoopActions
```

```
{
  [cellTotalCooperativeActions putValue: [cellTotalCooperativeActions getValueAtX: x
Y: y]+numCoopActions atX: x Y: y];

  return self;
}

-incrementTotalDiversityAtX: (int) x Y: (int) y Diversity: (double) diversity
{
  [cellTotalDiversity putValue: [cellTotalDiversity getValueAtX: x Y:
y]+(diversity*100) atX: x Y: y];
  [cellDiversityDivisor putValue: [cellDiversityDivisor getValueAtX: x Y: y]+1 atX: x
Y: y];

  return self;
}

-(double)getCooperationLevelAtX: (int) x Y: (int) y
{
  if ([cellTotalActions getValueAtX: x Y: y]==0)
  {
    return 0;
  }
  else
  {
    return (double)[cellTotalCooperativeActions getValueAtX: x Y:
y]/(double)[cellTotalActions getValueAtX: x Y: y];
  }
}

-(double)getDiversityLevelAtX: (int) x Y: (int) y
{
  if ([cellDiversityDivisor getValueAtX: x Y: y]==0)
  {
    return 0;
  }
  else
  {
    return ((double)[cellTotalDiversity getValueAtX: x Y:
y]/100)/(double)[cellDiversityDivisor getValueAtX: x Y: y];
  }
}

-resetCellTotalActions
{
  int x,y;
  for (x=0; x<xsize; x++)
  {
    for (y=0; y<ysize; y++)
    {
      [cellTotalActions putValue: 0 atX: x Y: y];
      [cellTotalCooperativeActions putValue: 0 atX: x Y: y];
    }
  }

  return self;
}

-resetCellTotalDiversity
{
  int x,y;
  for (x=0; x<xsize; x++)
  {
    for (y=0; y<ysize; y++)
    {
      [cellTotalDiversity putValue: 0 atX: x Y: y];
      [cellDiversityDivisor putValue: 0 atX: x Y: y];
    }
  }

  return self;
}

@end
```

DoubleData.h

```
//DoubleData.h Double wrapper for use with arrays

#import <objectbase/SwarmObject.h>

@interface DoubleData: SwarmObject
{
  double data;
}

-(double)getDoubleData;
-(void)setDoubleData: (double) newData;

@end
```

DoubleData.m

```
//DoubleData.h Double wrapper for use with arrays

#import "DoubleData.h"

@implementation DoubleData: SwarmObject
{
  double data;
}

-(double)getDoubleData
{
  return data;
}
-(void)setDoubleData: (double) newData;
{
  data=newData;
}

@end
```

IntegerData.h

```
//IntegerData.h Integer wrapper for use with arrays

#import <objectbase/SwarmObject.h>

@interface IntegerData: SwarmObject
{
  int data;
}

-(int)getIntData;
-(void)setIntData: (int) newData;

@end
```

IntegerData.m

```
//IntegerData.m Integer wrapper for use with arrays

#import "IntegerData.h"

@implementation IntegerData: SwarmObject
{
  int data;
}

-(int)getIntData
{
  return data;
}
-(void)setIntData: (int) newData;
{
  data=newData;
```

```
}

@end
```

experiment.setup

```
@begin
movementProbability 0
moveProbInc 0.1
moveProbMax 1
runNumber 1
runNumberMax 20
@end
```

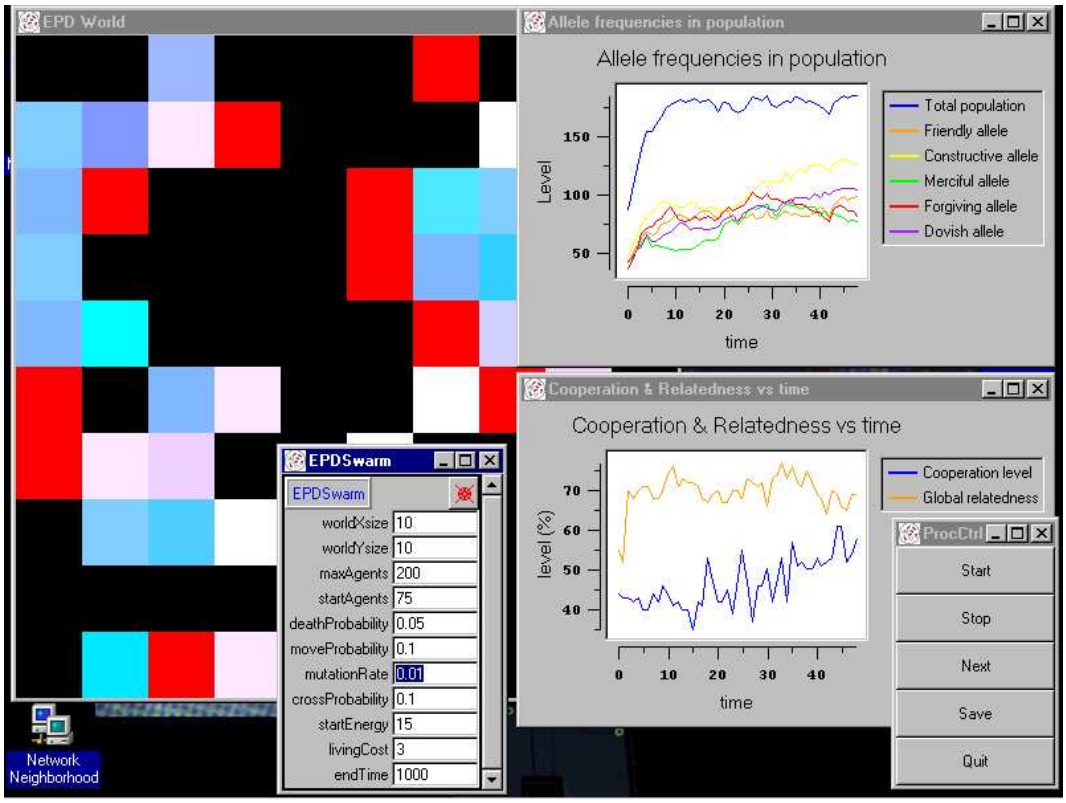
payoffs.setup

```
@begin
AAPayoff 3
ABPayoff 0
BAPayoff 5
BBPayoff 1
@end
```

world.setup

```
@begin
worldXsize 10
worldYsize 10
maxAgents 200
maxLocalAgents 5
startAgents 75
deathProbability 0.05
moveProbability 1
mutationRate 0.01
crossProbability 0.1
startEnergy 15
livingCost 3
endTime 1000
@end
```

Appendix C – Sample User Interface for the Observer Mode of the Evolutionary Prisoner's Dilemma



Appendix D – Experimental Data

This appendix contains the experimental data used to calculate the results presented in chapter 5.

Experiment 5.3.2

Movement probability	Average cooperation	Average relatedness	Average interaction length	Model time	Average cell population	Average number of partners
0.0	64	75	1.22E+00	1001	2.41E+01	7.52E+00
0.0	36	76	1.17E+00	1001	2.76E+01	8.01E+00
0.0	34	71	1.18E+00	1001	2.72E+01	7.70E+00
0.0	44	76	1.19E+00	1001	2.74E+01	7.80E+00
0.0	38	76	1.25E+00	1001	2.38E+01	7.41E+00
0.0	43	80	1.22E+00	1001	2.29E+01	7.50E+00
0.0	62	76	1.17E+00	1001	2.80E+01	7.94E+00
0.0	35	75	1.22E+00	1001	2.32E+01	7.63E+00
0.0	33	76	1.20E+00	1001	2.54E+01	7.76E+00
0.0	29	75	1.28E+00	1001	2.13E+01	7.28E+00
0.0	38	76	1.16E+00	1001	2.87E+01	7.75E+00
0.0	78	82	1.18E+00	1001	2.58E+01	7.68E+00
0.0	57	75	1.19E+00	1001	2.69E+01	7.69E+00
0.0	47	82	1.27E+00	1001	2.11E+01	7.14E+00
0.0	56	80	1.22E+00	1001	2.38E+01	7.50E+00
0.0	35	75	1.19E+00	1001	2.52E+01	7.64E+00
0.0	65	72	1.10E+00	1001	3.70E+01	8.50E+00
0.0	57	75	1.22E+00	1001	2.54E+01	7.57E+00
0.0	54	71	1.11E+00	1001	3.70E+01	8.29E+00
0.0	72	78	1.15E+00	1001	2.95E+01	8.07E+00
0.1	49	66	2.42E+00	1001	2.53E+00	2.95E+00
0.1	38	70	2.36E+00	1001	2.67E+00	3.09E+00
0.1	39	67	2.39E+00	1001	2.56E+00	2.98E+00
0.1	38	68	2.42E+00	1001	2.60E+00	3.04E+00
0.1	31	70	2.38E+00	1001	2.59E+00	2.99E+00
0.1	68	65	2.31E+00	1001	2.66E+00	3.11E+00
0.1	59	70	2.36E+00	1001	2.66E+00	3.01E+00
0.1	47	67	2.33E+00	1001	2.65E+00	3.07E+00
0.1	55	68	2.37E+00	1001	2.57E+00	2.98E+00
0.1	43	67	2.37E+00	1001	2.55E+00	2.96E+00
0.1	60	65	2.40E+00	1001	2.59E+00	3.03E+00
0.1	41	64	2.38E+00	1001	2.57E+00	2.98E+00
0.1	36	64	2.34E+00	1001	2.70E+00	3.07E+00
0.1	51	67	2.40E+00	1001	2.57E+00	3.00E+00
0.1	51	63	2.36E+00	1001	2.63E+00	3.03E+00
0.1	48	63	2.40E+00	1001	2.54E+00	2.95E+00
0.1	54	65	2.33E+00	1001	2.64E+00	3.02E+00
0.1	65	67	2.32E+00	1001	2.65E+00	3.06E+00
0.1	59	69	2.37E+00	1001	2.57E+00	2.99E+00
0.1	67	67	2.36E+00	1001	2.66E+00	3.06E+00
0.2	35	60	1.93E+00	1001	2.31E+00	3.63E+00
0.2	66	64	1.95E+00	1001	2.31E+00	3.60E+00
0.2	55	61	1.92E+00	1001	2.34E+00	3.61E+00
0.2	64	65	1.93E+00	1001	2.32E+00	3.59E+00
0.2	44	59	1.92E+00	1001	2.33E+00	3.58E+00
0.2	45	63	1.94E+00	1001	2.32E+00	3.62E+00
0.2	47	60	1.94E+00	1001	2.31E+00	3.62E+00
0.2	53	61	1.93E+00	1001	2.31E+00	3.58E+00
0.2	43	64	1.93E+00	1001	2.32E+00	3.61E+00

0.2	58	63	1.92E+00	1001	2.33E+00	3.63E+00
0.2	43	63	1.93E+00	1001	2.33E+00	3.63E+00
0.2	42	66	1.93E+00	1001	2.34E+00	3.63E+00
0.2	47	67	1.92E+00	1001	2.32E+00	3.62E+00
0.2	57	61	1.93E+00	1001	2.32E+00	3.62E+00
0.2	59	60	1.93E+00	1001	2.31E+00	3.58E+00
0.2	43	64	1.93E+00	1001	2.31E+00	3.62E+00
0.2	50	61	1.91E+00	1001	2.33E+00	3.56E+00
0.2	56	64	1.95E+00	1001	2.31E+00	3.59E+00
0.2	48	61	1.94E+00	1001	2.32E+00	3.59E+00
0.2	35	60	1.94E+00	1001	2.32E+00	3.63E+00
0.3	50	56	1.64E+00	1001	2.24E+00	4.31E+00
0.3	55	61	1.63E+00	1001	2.25E+00	4.22E+00
0.3	52	57	1.63E+00	1001	2.25E+00	4.19E+00
0.3	44	57	1.63E+00	1001	2.25E+00	4.17E+00
0.3	33	58	1.62E+00	1001	2.24E+00	4.21E+00
0.3	53	58	1.63E+00	1001	2.25E+00	4.27E+00
0.3	32	59	1.63E+00	1001	2.26E+00	4.26E+00
0.3	50	57	1.62E+00	1001	2.26E+00	4.27E+00
0.3	52	56	1.63E+00	1001	2.25E+00	4.28E+00
0.3	43	58	1.63E+00	1001	2.26E+00	4.26E+00
0.3	44	60	1.63E+00	1001	2.25E+00	4.24E+00
0.3	49	63	1.62E+00	1001	2.26E+00	4.25E+00
0.3	38	58	1.62E+00	1001	2.25E+00	4.26E+00
0.3	51	59	1.63E+00	1001	2.26E+00	4.28E+00
0.3	58	63	1.62E+00	1001	2.25E+00	4.25E+00
0.3	57	59	1.62E+00	1001	2.25E+00	4.27E+00
0.3	46	61	1.63E+00	1001	2.24E+00	4.22E+00
0.3	58	59	1.63E+00	1001	2.27E+00	4.28E+00
0.3	55	58	1.62E+00	1001	2.25E+00	4.20E+00
0.3	43	56	1.63E+00	1001	2.26E+00	4.23E+00
0.4	51	54	1.44E+00	1001	2.22E+00	4.83E+00
0.4	59	55	1.43E+00	1001	2.22E+00	4.82E+00
0.4	66	59	1.44E+00	1001	2.22E+00	4.87E+00
0.4	46	58	1.43E+00	1001	2.21E+00	4.73E+00
0.4	64	61	1.44E+00	1001	2.22E+00	4.83E+00
0.4	55	57	1.44E+00	1001	2.21E+00	4.82E+00
0.4	57	58	1.44E+00	1001	2.22E+00	4.69E+00
0.4	48	56	1.43E+00	1001	2.23E+00	4.76E+00
0.4	28	61	1.44E+00	1001	2.23E+00	4.82E+00
0.4	50	56	1.43E+00	1001	2.21E+00	4.80E+00
0.4	39	61	1.43E+00	1001	2.21E+00	4.80E+00
0.4	44	58	1.43E+00	1001	2.23E+00	4.80E+00
0.4	48	55	1.43E+00	1001	2.21E+00	4.85E+00
0.4	42	57	1.44E+00	1001	2.22E+00	4.78E+00
0.4	56	59	1.43E+00	1001	2.22E+00	4.82E+00
0.4	33	63	1.43E+00	1001	2.21E+00	4.82E+00
0.4	51	53	1.43E+00	1001	2.21E+00	4.74E+00
0.4	65	57	1.44E+00	1001	2.22E+00	4.82E+00
0.4	33	55	1.44E+00	1001	2.22E+00	4.76E+00
0.4	65	63	1.43E+00	1001	2.22E+00	4.76E+00
0.5	50	55	1.32E+00	1001	2.20E+00	5.25E+00
0.5	39	54	1.32E+00	1001	2.20E+00	5.39E+00
0.5	56	56	1.31E+00	1001	2.20E+00	5.36E+00
0.5	44	55	1.32E+00	1001	2.20E+00	5.19E+00
0.5	45	56	1.32E+00	1001	2.20E+00	5.25E+00
0.5	69	59	1.32E+00	1001	2.20E+00	5.39E+00
0.5	60	57	1.31E+00	1001	2.20E+00	5.25E+00

0.5	40	58	1.31E+00	1001	2.20E+00	5.33E+00
0.5	57	57	1.31E+00	1001	2.20E+00	5.25E+00
0.5	35	58	1.31E+00	1001	2.20E+00	5.28E+00
0.5	37	60	1.31E+00	1001	2.20E+00	5.24E+00
0.5	51	58	1.31E+00	1001	2.20E+00	5.20E+00
0.5	45	54	1.31E+00	1001	2.20E+00	5.29E+00
0.5	50	57	1.31E+00	1001	2.20E+00	5.31E+00
0.5	54	57	1.31E+00	1001	2.20E+00	5.27E+00
0.5	26	59	1.31E+00	1001	2.19E+00	5.14E+00
0.5	64	58	1.31E+00	1001	2.20E+00	5.27E+00
0.5	69	58	1.32E+00	1001	2.20E+00	5.31E+00
0.5	68	60	1.32E+00	1001	2.19E+00	5.31E+00
0.5	37	57	1.31E+00	1001	2.20E+00	5.26E+00
0.6	45	58	1.23E+00	1001	2.19E+00	5.63E+00
0.6	40	58	1.23E+00	1001	2.19E+00	5.66E+00
0.6	55	54	1.23E+00	1001	2.19E+00	5.64E+00
0.6	29	57	1.23E+00	1001	2.18E+00	5.60E+00
0.6	26	59	1.23E+00	1001	2.18E+00	5.70E+00
0.6	44	60	1.24E+00	1001	2.19E+00	5.75E+00
0.6	35	57	1.23E+00	1001	2.19E+00	5.68E+00
0.6	62	60	1.23E+00	1001	2.18E+00	5.70E+00
0.6	28	60	1.23E+00	1001	2.19E+00	5.54E+00
0.6	70	56	1.23E+00	1001	2.19E+00	5.54E+00
0.6	40	56	1.23E+00	1001	2.19E+00	5.64E+00
0.6	37	60	1.22E+00	1001	2.19E+00	5.57E+00
0.6	61	56	1.23E+00	1001	2.19E+00	5.63E+00
0.6	45	55	1.23E+00	1001	2.19E+00	5.62E+00
0.6	61	56	1.23E+00	1001	2.19E+00	5.66E+00
0.6	59	60	1.23E+00	1001	2.19E+00	5.59E+00
0.6	32	59	1.23E+00	1001	2.19E+00	5.55E+00
0.6	29	61	1.23E+00	1001	2.19E+00	5.55E+00
0.6	63	53	1.23E+00	1001	2.19E+00	5.58E+00
0.6	61	57	1.23E+00	1001	2.19E+00	5.64E+00
0.7	36	59	1.18E+00	1001	2.19E+00	5.83E+00
0.7	56	59	1.17E+00	1001	2.18E+00	5.75E+00
0.7	77	59	1.18E+00	1001	2.18E+00	5.82E+00
0.7	41	55	1.18E+00	1001	2.18E+00	5.99E+00
0.7	68	56	1.18E+00	1001	2.18E+00	5.82E+00
0.7	53	54	1.17E+00	1001	2.18E+00	5.87E+00
0.7	73	57	1.18E+00	1001	2.18E+00	5.83E+00
0.7	60	57	1.18E+00	1001	2.18E+00	5.90E+00
0.7	42	54	1.18E+00	1001	2.18E+00	5.75E+00
0.7	72	59	1.18E+00	1001	2.17E+00	5.76E+00
0.7	46	56	1.18E+00	1001	2.18E+00	5.87E+00
0.7	52	55	1.18E+00	1001	2.18E+00	5.90E+00
0.7	62	59	1.17E+00	1001	2.18E+00	5.83E+00
0.7	55	54	1.18E+00	1001	2.18E+00	5.84E+00
0.7	61	57	1.17E+00	1001	2.18E+00	5.76E+00
0.7	30	61	1.18E+00	1001	2.18E+00	5.95E+00
0.7	43	55	1.18E+00	1001	2.18E+00	5.79E+00
0.7	63	57	1.18E+00	1001	2.19E+00	5.93E+00
0.7	57	57	1.18E+00	1001	2.18E+00	5.81E+00
0.7	74	60	1.18E+00	1001	2.18E+00	5.70E+00
0.8	64	56	1.15E+00	1001	2.18E+00	6.01E+00
0.8	44	55	1.14E+00	1001	2.17E+00	5.93E+00
0.8	26	59	1.15E+00	1001	2.18E+00	6.00E+00
0.8	42	53	1.14E+00	1001	2.17E+00	5.98E+00
0.8	22	58	1.15E+00	1001	2.17E+00	5.92E+00

0.8	69	58	1.15E+00	1001	2.17E+00	6.04E+00
0.8	42	53	1.14E+00	1001	2.18E+00	6.02E+00
0.8	45	55	1.15E+00	1001	2.17E+00	5.88E+00
0.8	54	58	1.15E+00	1001	2.17E+00	5.91E+00
0.8	38	55	1.15E+00	1001	2.17E+00	5.95E+00
0.8	66	59	1.14E+00	1001	2.17E+00	5.92E+00
0.8	39	57	1.14E+00	1001	2.17E+00	5.81E+00
0.8	63	55	1.15E+00	1001	2.18E+00	6.09E+00
0.8	53	55	1.15E+00	1001	2.18E+00	6.01E+00
0.8	69	57	1.15E+00	1001	2.18E+00	5.97E+00
0.8	43	53	1.15E+00	1001	2.18E+00	6.12E+00
0.8	45	60	1.14E+00	1001	2.19E+00	5.98E+00
0.8	51	54	1.15E+00	1001	2.18E+00	6.07E+00
0.8	33	55	1.15E+00	1001	2.18E+00	6.02E+00
0.8	46	53	1.14E+00	1001	2.18E+00	6.05E+00
0.9	24	56	1.13E+00	1001	2.17E+00	5.95E+00
0.9	60	62	1.13E+00	1001	2.17E+00	5.93E+00
0.9	55	54	1.14E+00	1001	2.18E+00	6.15E+00
0.9	42	52	1.13E+00	1001	2.17E+00	6.05E+00
0.9	53	54	1.13E+00	1001	2.18E+00	6.19E+00
0.9	38	57	1.14E+00	1001	2.18E+00	6.12E+00
0.9	56	55	1.14E+00	1001	2.17E+00	6.13E+00
0.9	52	58	1.14E+00	1001	2.17E+00	6.09E+00
0.9	44	54	1.13E+00	1001	2.17E+00	6.08E+00
0.9	57	56	1.13E+00	1001	2.17E+00	6.06E+00
0.9	32	59	1.14E+00	1001	2.17E+00	6.00E+00
0.9	54	54	1.13E+00	1001	2.17E+00	6.04E+00
0.9	38	55	1.14E+00	1001	2.18E+00	6.14E+00
0.9	49	55	1.14E+00	1001	2.18E+00	6.14E+00
0.9	44	56	1.13E+00	1001	2.17E+00	5.95E+00
0.9	43	59	1.13E+00	1001	2.17E+00	6.06E+00
0.9	48	56	1.13E+00	1001	2.17E+00	5.89E+00
0.9	47	54	1.13E+00	1001	2.17E+00	6.04E+00
0.9	75	65	1.14E+00	1001	2.17E+00	6.11E+00
0.9	61	58	1.14E+00	1001	2.17E+00	6.17E+00
1.0	34	54	1.14E+00	1001	2.17E+00	6.07E+00
1.0	30	56	1.14E+00	1001	2.18E+00	6.04E+00
1.0	51	56	1.14E+00	1001	2.17E+00	5.91E+00
1.0	39	57	1.14E+00	1001	2.17E+00	6.11E+00
1.0	38	53	1.14E+00	1001	2.17E+00	5.96E+00
1.0	53	55	1.14E+00	1001	2.18E+00	6.08E+00
1.0	51	58	1.15E+00	1001	2.18E+00	6.05E+00
1.0	44	60	1.14E+00	1001	2.17E+00	5.97E+00
1.0	64	55	1.14E+00	1001	2.18E+00	5.92E+00
1.0	61	57	1.14E+00	1001	2.17E+00	6.06E+00
1.0	15	60	1.14E+00	1001	2.18E+00	6.03E+00
1.0	42	53	1.14E+00	1001	2.17E+00	5.99E+00
1.0	51	60	1.14E+00	1001	2.17E+00	5.99E+00
1.0	69	54	1.14E+00	1001	2.18E+00	5.93E+00
1.0	36	56	1.14E+00	1001	2.17E+00	5.91E+00
1.0	49	56	1.14E+00	1001	2.18E+00	5.97E+00
1.0	68	55	1.14E+00	1001	2.18E+00	6.08E+00
1.0	53	57	1.14E+00	1001	2.17E+00	6.01E+00
1.0	45	51	1.14E+00	1001	2.17E+00	6.08E+00
1.0	59	55	1.14E+00	1001	2.18E+00	6.04E+00

Experiment 5.4.2

Movement probability	Average cooperation	Average relatedness	Average interaction length	Model time	Average cell population	Average number of partners
0.0	17	72	1.02E+00	1001	5.56E+01	3.64E+00
0.0	34	72	1.02E+00	1001	7.22E+01	4.29E+00
0.0	13	71	1.01E+00	1001	7.78E+01	3.55E+00
0.0	34	68	1.02E+00	1001	7.25E+01	4.26E+00
0.0	35	73	1.02E+00	1001	7.06E+01	4.32E+00
0.0	43	72	1.02E+00	1001	7.21E+01	4.67E+00
0.0	15	69	1.01E+00	1001	6.98E+01	3.59E+00
0.0	25	70	1.01E+00	1001	7.78E+01	3.94E+00
0.0	44	72	1.04E+00	1001	5.72E+01	4.60E+00
0.0	30	68	1.01E+00	1001	8.24E+01	4.16E+00
0.0	17	68	1.01E+00	1001	8.05E+01	3.68E+00
0.0	49	71	1.02E+00	1001	7.65E+01	4.99E+00
0.0	40	70	1.01E+00	1001	8.52E+01	4.58E+00
0.0	22	73	1.02E+00	1001	6.74E+01	3.81E+00
0.0	33	73	1.03E+00	1001	5.80E+01	4.11E+00
0.0	29	69	1.01E+00	1001	8.48E+01	4.13E+00
0.0	45	72	1.03E+00	1001	7.34E+01	4.70E+00
0.0	35	77	1.01E+00	1001	7.95E+01	4.32E+00
0.0	70	74	1.05E+00	1001	5.42E+01	6.10E+00
0.0	31	73	1.02E+00	1001	7.20E+01	4.14E+00
0.1	37	71	1.34E+00	1001	4.69E+00	2.69E+00
0.1	50	71	1.42E+00	1001	4.63E+00	2.79E+00
0.1	55	80	1.49E+00	1001	4.23E+00	2.71E+00
0.1	65	72	1.52E+00	1001	4.79E+00	3.09E+00
0.1	30	71	1.30E+00	1001	4.57E+00	2.55E+00
0.1	72	75	1.58E+00	1001	4.77E+00	3.18E+00
0.1	84	80	1.72E+00	1001	4.34E+00	3.13E+00
0.1	29	77	1.29E+00	1001	4.55E+00	2.56E+00
0.1	53	73	1.46E+00	1001	4.40E+00	2.78E+00
0.1	34	74	1.31E+00	1001	4.90E+00	2.69E+00
0.1	40	72	1.35E+00	1001	4.90E+00	2.75E+00
0.1	62	72	1.52E+00	1001	4.63E+00	2.98E+00
0.1	60	76	1.53E+00	1001	4.35E+00	2.83E+00
0.1	51	73	1.45E+00	1001	4.58E+00	2.80E+00
0.1	59	71	1.49E+00	1001	4.35E+00	2.86E+00
0.1	49	72	1.40E+00	1001	4.57E+00	2.78E+00
0.1	36	73	1.33E+00	1001	4.54E+00	2.61E+00
0.1	61	72	1.51E+00	1001	4.45E+00	2.91E+00
0.1	23	73	1.25E+00	1001	4.87E+00	2.55E+00
0.1	61	75	1.53E+00	1001	4.40E+00	2.83E+00
0.2	24	70	1.30E+00	1001	3.46E+00	2.25E+00
0.2	13	74	1.25E+00	1001	3.48E+00	2.14E+00
0.2	19	72	1.28E+00	1001	3.41E+00	2.18E+00
0.2	18	73	1.28E+00	1001	3.39E+00	2.17E+00
0.2	14	75	1.26E+00	1001	3.46E+00	2.16E+00
0.2	22	70	1.30E+00	1001	3.40E+00	2.23E+00
0.2	21	71	1.29E+00	1001	3.50E+00	2.25E+00
0.2	24	69	1.30E+00	1001	3.37E+00	2.24E+00
0.2	13	76	1.25E+00	1001	3.46E+00	2.14E+00
0.2	29	73	1.31E+00	1001	3.50E+00	2.33E+00
0.2	22	72	1.30E+00	1001	3.32E+00	2.20E+00
0.2	20	70	1.28E+00	1001	3.45E+00	2.22E+00
0.2	15	75	1.27E+00	1001	3.34E+00	2.14E+00
0.2	17	73	1.28E+00	1001	3.40E+00	2.16E+00
0.2	14	74	1.26E+00	1001	3.47E+00	2.14E+00

0.2	18	72	1.28E+00	1001	3.41E+00	2.18E+00
0.2	18	74	1.28E+00	1001	3.45E+00	2.18E+00
0.2	20	69	1.28E+00	1001	3.49E+00	2.23E+00
0.2	16	71	1.26E+00	1001	3.49E+00	2.19E+00
0.2	18	74	1.28E+00	1001	3.49E+00	2.19E+00
0.3	10	71	1.22E+00	1001	2.85E+00	2.01E+00
0.3	13	72	1.23E+00	1001	2.87E+00	2.04E+00
0.3	16	70	1.24E+00	1001	2.86E+00	2.07E+00
0.3	14	73	1.23E+00	1001	2.88E+00	2.04E+00
0.3	15	69	1.25E+00	1001	2.80E+00	2.03E+00
0.3	13	70	1.24E+00	1001	2.84E+00	2.03E+00
0.3	18	71	1.24E+00	1001	2.90E+00	2.11E+00
0.3	13	73	1.24E+00	1001	2.86E+00	2.04E+00
0.3	13	70	1.23E+00	1001	2.85E+00	2.03E+00
0.3	16	70	1.25E+00	1001	2.96E+00	2.11E+00
0.3	18	69	1.25E+00	1001	2.91E+00	2.12E+00
0.3	16	71	1.24E+00	1001	2.87E+00	2.07E+00
0.3	15	71	1.24E+00	1001	2.91E+00	2.08E+00
0.3	13	69	1.24E+00	1001	2.84E+00	2.02E+00
0.3	19	70	1.24E+00	1001	2.94E+00	2.14E+00
0.3	10	69	1.22E+00	1001	2.93E+00	2.03E+00
0.3	13	69	1.23E+00	1001	2.93E+00	2.06E+00
0.3	13	70	1.23E+00	1001	2.89E+00	2.05E+00
0.3	11	74	1.23E+00	1001	2.96E+00	2.04E+00
0.3	13	68	1.23E+00	1001	2.85E+00	2.03E+00
0.4	11	71	1.19E+00	1001	2.54E+00	1.97E+00
0.4	11	72	1.19E+00	1001	2.54E+00	1.98E+00
0.4	10	70	1.19E+00	1001	2.57E+00	1.98E+00
0.4	10	67	1.19E+00	1001	2.59E+00	1.98E+00
0.4	12	70	1.19E+00	1001	2.53E+00	1.98E+00
0.4	11	71	1.19E+00	1001	2.53E+00	1.96E+00
0.4	10	70	1.19E+00	1001	2.55E+00	1.97E+00
0.4	14	71	1.20E+00	1001	2.52E+00	2.00E+00
0.4	9	72	1.19E+00	1001	2.47E+00	1.92E+00
0.4	12	69	1.19E+00	1001	2.53E+00	1.98E+00
0.4	10	72	1.19E+00	1001	2.56E+00	1.96E+00
0.4	9	71	1.18E+00	1001	2.57E+00	1.96E+00
0.4	11	69	1.19E+00	1001	2.54E+00	1.98E+00
0.4	10	70	1.19E+00	1001	2.55E+00	1.97E+00
0.4	11	73	1.19E+00	1001	2.51E+00	1.96E+00
0.4	11	68	1.19E+00	1001	2.54E+00	1.99E+00
0.4	8	73	1.18E+00	1001	2.54E+00	1.94E+00
0.4	12	69	1.19E+00	1001	2.65E+00	2.02E+00
0.4	8	76	1.18E+00	1001	2.54E+00	1.94E+00
0.4	16	69	1.21E+00	1001	2.47E+00	1.98E+00
0.5	7	70	1.14E+00	1001	2.38E+00	1.94E+00
0.5	10	70	1.15E+00	1001	2.34E+00	1.95E+00
0.5	9	69	1.15E+00	1001	2.36E+00	1.94E+00
0.5	9	72	1.15E+00	1001	2.29E+00	1.91E+00
0.5	6	71	1.14E+00	1001	2.35E+00	1.91E+00
0.5	9	70	1.15E+00	1001	2.34E+00	1.92E+00
0.5	10	69	1.15E+00	1001	2.27E+00	1.92E+00
0.5	8	69	1.14E+00	1001	2.35E+00	1.93E+00
0.5	8	71	1.15E+00	1001	2.31E+00	1.91E+00
0.5	11	70	1.15E+00	1001	2.36E+00	1.97E+00
0.5	8	71	1.15E+00	1001	2.31E+00	1.92E+00
0.5	12	69	1.15E+00	1001	2.33E+00	1.98E+00
0.5	9	71	1.15E+00	1001	2.37E+00	1.95E+00

0.5	11	70	1.15E+00	1001	2.29E+00	1.94E+00
0.5	8	73	1.15E+00	1001	2.33E+00	1.90E+00
0.5	6	70	1.14E+00	1001	2.30E+00	1.87E+00
0.5	7	70	1.15E+00	1001	2.31E+00	1.91E+00
0.5	9	70	1.15E+00	1001	2.32E+00	1.93E+00
0.5	9	71	1.15E+00	1001	2.35E+00	1.94E+00
0.5	7	73	1.14E+00	1001	2.34E+00	1.91E+00
0.6	7	70	1.12E+00	1001	2.14E+00	1.86E+00
0.6	7	71	1.11E+00	1001	2.13E+00	1.86E+00
0.6	9	69	1.11E+00	1001	2.14E+00	1.90E+00
0.6	8	68	1.12E+00	1001	2.18E+00	1.91E+00
0.6	6	73	1.11E+00	1001	2.21E+00	1.89E+00
0.6	5	72	1.11E+00	1001	2.15E+00	1.86E+00
0.6	7	71	1.11E+00	1001	2.14E+00	1.87E+00
0.6	6	68	1.12E+00	1001	2.14E+00	1.87E+00
0.6	6	69	1.11E+00	1001	2.17E+00	1.89E+00
0.6	7	66	1.11E+00	1001	2.16E+00	1.88E+00
0.6	7	70	1.11E+00	1001	2.18E+00	1.89E+00
0.6	5	72	1.11E+00	1001	2.21E+00	1.89E+00
0.6	7	70	1.11E+00	1001	2.15E+00	1.87E+00
0.6	7	70	1.11E+00	1001	2.18E+00	1.90E+00
0.6	8	69	1.12E+00	1001	2.14E+00	1.87E+00
0.6	9	70	1.12E+00	1001	2.14E+00	1.89E+00
0.6	6	70	1.12E+00	1001	2.12E+00	1.85E+00
0.6	6	72	1.11E+00	1001	2.15E+00	1.86E+00
0.6	9	67	1.12E+00	1001	2.14E+00	1.88E+00
0.6	6	71	1.11E+00	1001	2.17E+00	1.87E+00
0.7	8	68	1.09E+00	1001	2.05E+00	1.87E+00
0.7	5	71	1.09E+00	1001	2.02E+00	1.83E+00
0.7	6	71	1.09E+00	1001	2.04E+00	1.84E+00
0.7	7	66	1.09E+00	1001	2.04E+00	1.86E+00
0.7	6	70	1.09E+00	1001	2.06E+00	1.85E+00
0.7	6	67	1.09E+00	1001	2.04E+00	1.84E+00
0.7	7	70	1.09E+00	1001	2.03E+00	1.86E+00
0.7	5	71	1.09E+00	1001	2.04E+00	1.84E+00
0.7	5	72	1.09E+00	1001	2.03E+00	1.82E+00
0.7	6	70	1.09E+00	1001	2.01E+00	1.82E+00
0.7	8	68	1.09E+00	1001	2.04E+00	1.86E+00
0.7	6	71	1.09E+00	1001	2.00E+00	1.82E+00
0.7	5	72	1.09E+00	1001	2.07E+00	1.85E+00
0.7	6	70	1.09E+00	1001	2.04E+00	1.85E+00
0.7	6	68	1.09E+00	1001	2.05E+00	1.86E+00
0.7	6	70	1.09E+00	1001	2.05E+00	1.85E+00
0.7	6	72	1.09E+00	1001	2.06E+00	1.86E+00
0.7	6	71	1.09E+00	1001	2.05E+00	1.85E+00
0.7	8	68	1.09E+00	1001	2.03E+00	1.86E+00
0.7	7	66	1.09E+00	1001	2.04E+00	1.86E+00
0.8	6	66	1.07E+00	1001	1.95E+00	1.82E+00
0.8	5	70	1.07E+00	1001	1.95E+00	1.81E+00
0.8	5	69	1.07E+00	1001	1.94E+00	1.80E+00
0.8	6	65	1.07E+00	1001	1.99E+00	1.84E+00
0.8	5	69	1.08E+00	1001	1.98E+00	1.84E+00
0.8	6	65	1.07E+00	1001	1.95E+00	1.84E+00
0.8	5	70	1.07E+00	1001	1.97E+00	1.82E+00
0.8	5	71	1.07E+00	1001	1.94E+00	1.81E+00
0.8	7	68	1.08E+00	1001	1.98E+00	1.86E+00
0.8	6	68	1.07E+00	1001	1.98E+00	1.84E+00
0.8	6	66	1.08E+00	1001	1.97E+00	1.83E+00

0.8	5	69	1.07E+00	1001	1.93E+00	1.79E+00
0.8	5	71	1.07E+00	1001	1.97E+00	1.82E+00
0.8	5	67	1.07E+00	1001	1.92E+00	1.78E+00
0.8	4	68	1.08E+00	1001	1.95E+00	1.80E+00
0.8	4	72	1.07E+00	1001	1.97E+00	1.81E+00
0.8	6	67	1.08E+00	1001	1.97E+00	1.84E+00
0.8	5	70	1.07E+00	1001	1.97E+00	1.82E+00
0.8	7	67	1.07E+00	1001	1.98E+00	1.85E+00
0.8	6	68	1.08E+00	1001	1.96E+00	1.82E+00
0.9	5	70	1.07E+00	1001	1.92E+00	1.81E+00
0.9	4	72	1.07E+00	1001	1.90E+00	1.77E+00
0.9	6	70	1.07E+00	1001	1.92E+00	1.79E+00
0.9	5	68	1.07E+00	1001	1.92E+00	1.80E+00
0.9	5	67	1.07E+00	1001	1.90E+00	1.80E+00
0.9	5	71	1.07E+00	1001	1.92E+00	1.79E+00
0.9	6	67	1.07E+00	1001	1.90E+00	1.80E+00
0.9	7	69	1.07E+00	1001	1.91E+00	1.81E+00
0.9	7	66	1.07E+00	1001	1.91E+00	1.81E+00
0.9	5	69	1.07E+00	1001	1.92E+00	1.80E+00
0.9	5	70	1.07E+00	1001	1.91E+00	1.79E+00
0.9	7	67	1.07E+00	1001	1.89E+00	1.79E+00
0.9	7	66	1.07E+00	1001	1.94E+00	1.81E+00
0.9	5	67	1.07E+00	1001	1.91E+00	1.78E+00
0.9	6	66	1.07E+00	1001	1.91E+00	1.79E+00
0.9	6	66	1.07E+00	1001	1.91E+00	1.81E+00
0.9	5	66	1.07E+00	1001	1.91E+00	1.80E+00
0.9	5	69	1.07E+00	1001	1.92E+00	1.79E+00
0.9	6	67	1.07E+00	1001	1.92E+00	1.81E+00
0.9	6	69	1.07E+00	1001	1.89E+00	1.79E+00
1.0	5	69	1.08E+00	1001	1.88E+00	1.76E+00
1.0	5	70	1.08E+00	1001	1.88E+00	1.75E+00
1.0	6	67	1.08E+00	1001	1.87E+00	1.76E+00
1.0	5	70	1.08E+00	1001	1.88E+00	1.76E+00
1.0	6	69	1.08E+00	1001	1.88E+00	1.77E+00
1.0	5	70	1.08E+00	1001	1.89E+00	1.76E+00
1.0	7	70	1.08E+00	1001	1.88E+00	1.76E+00
1.0	5	71	1.08E+00	1001	1.88E+00	1.77E+00
1.0	6	65	1.08E+00	1001	1.89E+00	1.79E+00
1.0	5	69	1.08E+00	1001	1.88E+00	1.75E+00
1.0	7	64	1.08E+00	1001	1.88E+00	1.77E+00
1.0	4	70	1.08E+00	1001	1.87E+00	1.74E+00
1.0	6	67	1.08E+00	1001	1.89E+00	1.77E+00
1.0	4	70	1.08E+00	1001	1.88E+00	1.74E+00
1.0	5	69	1.08E+00	1001	1.88E+00	1.76E+00
1.0	6	67	1.08E+00	1001	1.89E+00	1.78E+00
1.0	5	68	1.08E+00	1001	1.89E+00	1.77E+00
1.0	6	65	1.08E+00	1001	1.89E+00	1.77E+00
1.0	5	67	1.08E+00	1001	1.89E+00	1.77E+00
1.0	5	69	1.08E+00	1001	1.86E+00	1.75E+00

Experiment 5.4.3

Movement probability	Average cooperation	Average relatedness	Average interaction length	Model time	Average cell population	Average number of partners
0.00	17	72	1.02E+00	1001	5.56E+01	3.64E+00
0.00	34	72	1.02E+00	1001	7.22E+01	4.29E+00
0.00	13	71	1.01E+00	1001	7.78E+01	3.55E+00
0.00	34	68	1.02E+00	1001	7.25E+01	4.26E+00
0.00	35	73	1.02E+00	1001	7.06E+01	4.32E+00

0.00	43	72	1.02E+00	1001	7.21E+01	4.67E+00
0.00	15	69	1.01E+00	1001	6.98E+01	3.59E+00
0.00	25	70	1.01E+00	1001	7.78E+01	3.94E+00
0.00	44	72	1.04E+00	1001	5.72E+01	4.60E+00
0.00	30	68	1.01E+00	1001	8.24E+01	4.16E+00
0.00	17	68	1.01E+00	1001	8.05E+01	3.68E+00
0.00	49	71	1.02E+00	1001	7.65E+01	4.99E+00
0.00	40	70	1.01E+00	1001	8.52E+01	4.58E+00
0.00	22	73	1.02E+00	1001	6.74E+01	3.81E+00
0.00	33	73	1.03E+00	1001	5.80E+01	4.11E+00
0.00	29	69	1.01E+00	1001	8.48E+01	4.13E+00
0.00	45	72	1.03E+00	1001	7.34E+01	4.70E+00
0.00	35	77	1.01E+00	1001	7.95E+01	4.32E+00
0.00	70	74	1.05E+00	1001	5.42E+01	6.10E+00
0.00	31	73	1.02E+00	1001	7.20E+01	4.14E+00
0.02	84	79	1.33E+00	1001	9.47E+00	4.90E+00
0.02	81	76	1.28E+00	1001	1.01E+01	5.01E+00
0.02	80	77	1.23E+00	1001	1.15E+01	5.26E+00
0.02	87	79	1.38E+00	1001	1.01E+01	5.04E+00
0.02	74	79	1.21E+00	1001	1.07E+01	4.88E+00
0.02	84	79	1.32E+00	1001	9.25E+00	4.92E+00
0.02	84	80	1.32E+00	1001	9.87E+00	5.04E+00
0.02	74	78	1.28E+00	1001	9.90E+00	4.63E+00
0.02	88	79	1.43E+00	1001	8.91E+00	4.79E+00
0.02	50	78	1.15E+00	1001	1.08E+01	3.96E+00
0.02	77	78	1.27E+00	1001	9.77E+00	4.76E+00
0.02	87	80	1.45E+00	1001	8.86E+00	4.72E+00
0.02	83	76	1.34E+00	1001	1.02E+01	4.82E+00
0.02	75	71	1.22E+00	1001	1.12E+01	4.91E+00
0.02	81	77	1.31E+00	1001	9.88E+00	4.87E+00
0.02	83	77	1.29E+00	1001	1.07E+01	5.14E+00
0.02	88	79	1.34E+00	1001	1.04E+01	5.19E+00
0.02	84	80	1.32E+00	1001	1.01E+01	5.02E+00
0.02	81	80	1.33E+00	1001	9.35E+00	4.72E+00
0.02	72	75	1.16E+00	1001	1.19E+01	4.98E+00
0.04	78	79	1.50E+00	1001	6.61E+00	3.81E+00
0.04	75	80	1.47E+00	1001	6.33E+00	3.71E+00
0.04	84	76	1.55E+00	1001	7.03E+00	4.09E+00
0.04	75	80	1.50E+00	1001	6.10E+00	3.61E+00
0.04	83	79	1.55E+00	1001	6.61E+00	3.93E+00
0.04	81	79	1.53E+00	1001	6.76E+00	3.90E+00
0.04	77	77	1.47E+00	1001	7.05E+00	3.97E+00
0.04	69	76	1.35E+00	1001	7.73E+00	3.97E+00
0.04	86	82	1.60E+00	1001	6.45E+00	3.90E+00
0.04	81	72	1.46E+00	1001	7.51E+00	4.23E+00
0.04	87	78	1.64E+00	1001	6.37E+00	3.87E+00
0.04	75	79	1.41E+00	1001	7.17E+00	4.02E+00
0.04	72	77	1.44E+00	1001	6.51E+00	3.70E+00
0.04	80	78	1.53E+00	1001	6.51E+00	3.84E+00
0.04	85	82	1.57E+00	1001	6.27E+00	3.83E+00
0.04	82	81	1.59E+00	1001	6.15E+00	3.72E+00
0.04	81	81	1.51E+00	1001	6.39E+00	3.89E+00
0.04	57	77	1.26E+00	1001	7.66E+00	3.73E+00
0.04	85	80	1.59E+00	1001	6.74E+00	3.97E+00
0.04	85	78	1.59E+00	1001	6.48E+00	3.83E+00
0.06	59	74	1.44E+00	1001	5.55E+00	3.17E+00
0.06	73	76	1.52E+00	1001	5.65E+00	3.41E+00
0.06	73	74	1.52E+00	1001	5.67E+00	3.43E+00

0.06	62	74	1.43E+00	1001	5.58E+00	3.25E+00
0.06	68	74	1.48E+00	1001	5.58E+00	3.35E+00
0.06	44	74	1.29E+00	1001	6.13E+00	3.12E+00
0.06	80	78	1.58E+00	1001	5.79E+00	3.60E+00
0.06	76	75	1.58E+00	1001	5.30E+00	3.38E+00
0.06	70	73	1.50E+00	1001	5.80E+00	3.45E+00
0.06	71	74	1.48E+00	1001	6.04E+00	3.49E+00
0.06	79	77	1.62E+00	1001	5.93E+00	3.59E+00
0.06	48	74	1.32E+00	1001	5.96E+00	3.14E+00
0.06	40	77	1.27E+00	1001	6.00E+00	3.05E+00
0.06	72	72	1.51E+00	1001	5.84E+00	3.47E+00
0.06	78	78	1.55E+00	1001	5.77E+00	3.49E+00
0.06	76	75	1.54E+00	1001	5.73E+00	3.53E+00
0.06	35	74	1.25E+00	1001	6.08E+00	2.94E+00
0.06	69	76	1.51E+00	1001	5.54E+00	3.31E+00
0.06	62	77	1.44E+00	1001	5.46E+00	3.17E+00
0.06	63	76	1.41E+00	1001	6.17E+00	3.42E+00
0.08	63	73	1.46E+00	1001	5.16E+00	3.15E+00
0.08	42	70	1.34E+00	1001	5.12E+00	2.84E+00
0.08	52	77	1.43E+00	1001	4.89E+00	2.90E+00
0.08	79	78	1.67E+00	1001	4.89E+00	3.25E+00
0.08	67	73	1.53E+00	1001	4.81E+00	3.08E+00
0.08	52	74	1.41E+00	1001	5.19E+00	2.95E+00
0.08	73	70	1.57E+00	1001	5.27E+00	3.31E+00
0.08	59	72	1.46E+00	1001	5.04E+00	3.06E+00
0.08	68	73	1.52E+00	1001	5.16E+00	3.22E+00
0.08	41	74	1.32E+00	1001	5.27E+00	2.92E+00
0.08	47	75	1.38E+00	1001	4.99E+00	2.86E+00
0.08	39	73	1.33E+00	1001	5.17E+00	2.82E+00
0.08	54	72	1.40E+00	1001	5.18E+00	3.02E+00
0.08	85	75	1.68E+00	1001	5.15E+00	3.39E+00
0.08	80	81	1.62E+00	1001	4.99E+00	3.27E+00
0.08	21	75	1.21E+00	1001	5.49E+00	2.66E+00
0.08	44	73	1.37E+00	1001	5.11E+00	2.82E+00
0.08	77	73	1.64E+00	1001	4.88E+00	3.23E+00
0.08	47	72	1.39E+00	1001	5.02E+00	2.87E+00
0.08	49	76	1.39E+00	1001	5.05E+00	2.88E+00
0.10	39	75	1.34E+00	1001	4.69E+00	2.72E+00
0.10	59	72	1.48E+00	1001	4.49E+00	2.89E+00
0.10	55	75	1.48E+00	1001	4.26E+00	2.74E+00
0.10	45	72	1.35E+00	1001	4.97E+00	2.87E+00
0.10	58	74	1.49E+00	1001	4.47E+00	2.86E+00
0.10	35	71	1.33E+00	1001	4.72E+00	2.64E+00
0.10	45	74	1.39E+00	1001	4.69E+00	2.76E+00
0.10	25	75	1.28E+00	1001	4.52E+00	2.50E+00
0.10	34	75	1.31E+00	1001	4.70E+00	2.66E+00
0.10	50	70	1.43E+00	1001	4.66E+00	2.80E+00
0.10	41	73	1.38E+00	1001	4.36E+00	2.61E+00
0.10	84	75	1.69E+00	1001	4.47E+00	3.18E+00
0.10	47	73	1.42E+00	1001	4.57E+00	2.80E+00
0.10	48	73	1.41E+00	1001	4.45E+00	2.76E+00
0.10	57	75	1.48E+00	1001	4.58E+00	2.89E+00
0.10	25	74	1.28E+00	1001	4.48E+00	2.48E+00
0.10	54	75	1.45E+00	1001	4.68E+00	2.88E+00
0.10	47	72	1.40E+00	1001	4.63E+00	2.79E+00
0.10	65	74	1.55E+00	1001	4.63E+00	3.01E+00
0.10	50	75	1.44E+00	1001	4.52E+00	2.76E+00
0.12	36	72	1.34E+00	1001	4.19E+00	2.54E+00

0.12	43	73	1.39E+00	1001	4.26E+00	2.65E+00
0.12	36	74	1.34E+00	1001	4.24E+00	2.56E+00
0.12	31	71	1.32E+00	1001	4.34E+00	2.54E+00
0.12	50	71	1.45E+00	1001	4.25E+00	2.70E+00
0.12	25	71	1.29E+00	1001	4.28E+00	2.44E+00
0.12	23	71	1.28E+00	1001	4.31E+00	2.44E+00
0.12	46	74	1.42E+00	1001	4.27E+00	2.67E+00
0.12	45	69	1.40E+00	1001	4.31E+00	2.70E+00
0.12	29	72	1.31E+00	1001	4.13E+00	2.44E+00
0.12	71	75	1.61E+00	1001	4.10E+00	2.92E+00
0.12	43	66	1.40E+00	1001	4.21E+00	2.63E+00
0.12	24	71	1.28E+00	1001	4.30E+00	2.44E+00
0.12	52	71	1.46E+00	1001	4.23E+00	2.74E+00
0.12	62	70	1.53E+00	1001	4.16E+00	2.82E+00
0.12	19	74	1.26E+00	1001	4.33E+00	2.39E+00
0.12	27	75	1.30E+00	1001	4.26E+00	2.48E+00
0.12	49	72	1.44E+00	1001	4.30E+00	2.76E+00
0.12	57	74	1.50E+00	1001	4.18E+00	2.79E+00
0.12	58	75	1.52E+00	1001	4.09E+00	2.77E+00
0.14	36	68	1.35E+00	1001	4.06E+00	2.53E+00
0.14	37	71	1.37E+00	1001	3.97E+00	2.51E+00
0.14	24	77	1.30E+00	1001	4.00E+00	2.37E+00
0.14	37	80	1.37E+00	1001	3.82E+00	2.44E+00
0.14	53	70	1.44E+00	1001	4.09E+00	2.75E+00
0.14	38	73	1.36E+00	1001	4.14E+00	2.55E+00
0.14	32	68	1.34E+00	1001	4.09E+00	2.50E+00
0.14	31	73	1.33E+00	1001	4.04E+00	2.44E+00
0.14	47	70	1.42E+00	1001	3.95E+00	2.63E+00
0.14	24	73	1.29E+00	1001	3.99E+00	2.39E+00
0.14	27	73	1.32E+00	1001	3.92E+00	2.37E+00
0.14	32	72	1.34E+00	1001	4.15E+00	2.48E+00
0.14	35	70	1.37E+00	1001	3.98E+00	2.49E+00
0.14	34	70	1.36E+00	1001	3.96E+00	2.47E+00
0.14	29	71	1.32E+00	1001	4.05E+00	2.45E+00
0.14	34	73	1.36E+00	1001	3.81E+00	2.40E+00
0.14	40	70	1.39E+00	1001	3.92E+00	2.53E+00
0.14	42	70	1.39E+00	1001	4.02E+00	2.57E+00
0.14	33	71	1.34E+00	1001	3.96E+00	2.47E+00
0.14	23	71	1.29E+00	1001	4.05E+00	2.39E+00
0.16	28	73	1.32E+00	1001	3.72E+00	2.35E+00
0.16	28	72	1.32E+00	1001	3.77E+00	2.35E+00
0.16	34	72	1.36E+00	1001	3.69E+00	2.39E+00
0.16	22	72	1.29E+00	1001	3.81E+00	2.31E+00
0.16	29	70	1.33E+00	1001	3.68E+00	2.34E+00
0.16	22	71	1.29E+00	1001	3.85E+00	2.32E+00
0.16	18	73	1.27E+00	1001	3.82E+00	2.26E+00
0.16	24	70	1.30E+00	1001	3.81E+00	2.33E+00
0.16	25	72	1.29E+00	1001	3.91E+00	2.36E+00
0.16	18	73	1.27E+00	1001	3.77E+00	2.26E+00
0.16	32	70	1.34E+00	1001	3.71E+00	2.39E+00
0.16	29	71	1.33E+00	1001	3.78E+00	2.38E+00
0.16	41	72	1.39E+00	1001	3.74E+00	2.46E+00
0.16	49	71	1.44E+00	1001	3.65E+00	2.57E+00
0.16	30	70	1.32E+00	1001	3.84E+00	2.40E+00
0.16	20	71	1.29E+00	1001	3.76E+00	2.27E+00
0.16	28	72	1.33E+00	1001	3.71E+00	2.35E+00
0.16	17	72	1.27E+00	1001	3.82E+00	2.27E+00
0.16	16	72	1.26E+00	1001	3.88E+00	2.27E+00

0.16	26	68	1.30E+00	1001	3.88E+00	2.37E+00
0.18	31	71	1.35E+00	1001	3.57E+00	2.35E+00
0.18	19	72	1.28E+00	1001	3.57E+00	2.21E+00
0.18	21	74	1.30E+00	1001	3.53E+00	2.23E+00
0.18	22	74	1.28E+00	1001	3.76E+00	2.32E+00
0.18	24	74	1.31E+00	1001	3.60E+00	2.30E+00
0.18	20	74	1.28E+00	1001	3.66E+00	2.26E+00
0.18	16	73	1.28E+00	1001	3.50E+00	2.16E+00
0.18	48	70	1.41E+00	1001	3.54E+00	2.55E+00
0.18	17	73	1.28E+00	1001	3.57E+00	2.20E+00
0.18	24	72	1.30E+00	1001	3.59E+00	2.28E+00
0.18	25	73	1.31E+00	1001	3.61E+00	2.30E+00
0.18	26	73	1.31E+00	1001	3.52E+00	2.28E+00
0.18	17	72	1.26E+00	1001	3.73E+00	2.26E+00
0.18	15	74	1.25E+00	1001	3.70E+00	2.23E+00
0.18	22	74	1.30E+00	1001	3.60E+00	2.25E+00
0.18	22	73	1.30E+00	1001	3.49E+00	2.22E+00
0.18	24	71	1.30E+00	1001	3.66E+00	2.29E+00
0.18	18	72	1.27E+00	1001	3.66E+00	2.23E+00
0.18	27	70	1.32E+00	1001	3.67E+00	2.34E+00
0.18	24	74	1.30E+00	1001	3.63E+00	2.28E+00
0.20	22	70	1.30E+00	1001	3.32E+00	2.19E+00
0.20	16	71	1.26E+00	1001	3.53E+00	2.19E+00
0.20	15	75	1.26E+00	1001	3.42E+00	2.15E+00
0.20	23	68	1.30E+00	1001	3.45E+00	2.24E+00
0.20	14	72	1.26E+00	1001	3.48E+00	2.16E+00
0.20	25	70	1.30E+00	1001	3.54E+00	2.29E+00
0.20	19	70	1.29E+00	1001	3.45E+00	2.20E+00
0.20	22	77	1.29E+00	1001	3.38E+00	2.21E+00
0.20	16	73	1.28E+00	1001	3.38E+00	2.13E+00
0.20	21	70	1.29E+00	1001	3.35E+00	2.18E+00
0.20	23	71	1.30E+00	1001	3.41E+00	2.26E+00
0.20	14	74	1.26E+00	1001	3.48E+00	2.16E+00
0.20	19	71	1.28E+00	1001	3.47E+00	2.21E+00
0.20	23	72	1.30E+00	1001	3.42E+00	2.24E+00
0.20	17	72	1.27E+00	1001	3.48E+00	2.19E+00
0.20	21	71	1.29E+00	1001	3.43E+00	2.21E+00
0.20	17	73	1.28E+00	1001	3.39E+00	2.16E+00
0.20	19	72	1.28E+00	1001	3.50E+00	2.22E+00
0.20	22	70	1.29E+00	1001	3.47E+00	2.26E+00
0.20	29	74	1.33E+00	1001	3.38E+00	2.31E+00

Experiment 5.4.4

Movement probability	Average cooperation	Average relatedness	Average interaction length	Model time	Average cell population	Average number of partners
0.000	17	72	1.02E+00	1001	5.56E+01	3.64E+00
0.000	34	72	1.02E+00	1001	7.22E+01	4.29E+00
0.000	13	71	1.01E+00	1001	7.78E+01	3.55E+00
0.000	34	68	1.02E+00	1001	7.25E+01	4.26E+00
0.000	35	73	1.02E+00	1001	7.06E+01	4.32E+00
0.000	43	72	1.02E+00	1001	7.21E+01	4.67E+00
0.000	15	69	1.01E+00	1001	6.98E+01	3.59E+00
0.000	25	70	1.01E+00	1001	7.78E+01	3.94E+00
0.000	44	72	1.04E+00	1001	5.72E+01	4.60E+00
0.000	30	68	1.01E+00	1001	8.24E+01	4.16E+00
0.000	17	68	1.01E+00	1001	8.05E+01	3.68E+00
0.000	49	71	1.02E+00	1001	7.65E+01	4.99E+00
0.000	40	70	1.01E+00	1001	8.52E+01	4.58E+00

0.000	22	73	1.02E+00	1001	6.74E+01	3.81E+00
0.000	33	73	1.03E+00	1001	5.80E+01	4.11E+00
0.000	29	69	1.01E+00	1001	8.48E+01	4.13E+00
0.000	45	72	1.03E+00	1001	7.34E+01	4.70E+00
0.000	35	77	1.01E+00	1001	7.95E+01	4.32E+00
0.000	70	74	1.05E+00	1001	5.42E+01	6.10E+00
0.000	31	73	1.02E+00	1001	7.20E+01	4.14E+00
0.002	75	76	1.06E+00	1001	3.66E+01	6.18E+00
0.002	50	70	1.02E+00	1001	4.26E+01	4.90E+00
0.002	66	72	1.03E+00	1001	3.90E+01	5.69E+00
0.002	10	69	1.01E+00	1001	4.71E+01	3.40E+00
0.002	42	72	1.03E+00	1001	4.21E+01	4.45E+00
0.002	37	70	1.04E+00	1001	3.97E+01	4.21E+00
0.002	41	68	1.02E+00	1001	4.79E+01	4.51E+00
0.002	35	72	1.02E+00	1001	4.22E+01	4.20E+00
0.002	45	76	1.02E+00	1001	4.34E+01	4.70E+00
0.002	44	69	1.04E+00	1001	3.57E+01	4.51E+00
0.002	26	69	1.02E+00	1001	4.03E+01	3.87E+00
0.002	24	73	1.02E+00	1001	4.37E+01	3.79E+00
0.002	68	65	1.03E+00	1001	4.45E+01	5.96E+00
0.002	32	74	1.02E+00	1001	4.54E+01	4.09E+00
0.002	33	77	1.04E+00	1001	3.44E+01	4.03E+00
0.002	42	70	1.04E+00	1001	4.20E+01	4.47E+00
0.002	47	76	1.05E+00	1001	3.44E+01	4.60E+00
0.002	29	72	1.02E+00	1001	4.23E+01	4.01E+00
0.002	59	73	1.05E+00	1001	3.58E+01	5.24E+00
0.002	27	72	1.02E+00	1001	4.13E+01	3.89E+00
0.004	77	73	1.06E+00	1001	2.64E+01	6.22E+00
0.004	78	73	1.04E+00	1001	2.84E+01	6.41E+00
0.004	40	76	1.05E+00	1001	2.54E+01	4.22E+00
0.004	33	71	1.03E+00	1001	2.90E+01	4.06E+00
0.004	59	74	1.05E+00	1001	2.73E+01	5.08E+00
0.004	38	73	1.03E+00	1001	2.69E+01	4.27E+00
0.004	63	75	1.05E+00	1001	2.72E+01	5.40E+00
0.004	37	75	1.02E+00	1001	2.98E+01	4.23E+00
0.004	38	71	1.03E+00	1001	3.06E+01	4.24E+00
0.004	63	74	1.04E+00	1001	3.03E+01	5.40E+00
0.004	65	78	1.05E+00	1001	2.54E+01	5.45E+00
0.004	37	72	1.04E+00	1001	3.01E+01	4.18E+00
0.004	37	75	1.03E+00	1001	2.82E+01	4.17E+00
0.004	31	76	1.03E+00	1001	2.88E+01	3.98E+00
0.004	73	74	1.07E+00	1001	2.66E+01	5.90E+00
0.004	23	71	1.03E+00	1001	3.15E+01	3.74E+00
0.004	84	79	1.08E+00	1001	2.59E+01	6.74E+00
0.004	33	71	1.02E+00	1001	3.25E+01	4.03E+00
0.004	81	75	1.06E+00	1001	2.69E+01	6.58E+00
0.004	74	74	1.06E+00	1001	2.76E+01	6.11E+00
0.006	77	77	1.11E+00	1001	1.86E+01	5.81E+00
0.006	43	76	1.04E+00	1001	2.13E+01	4.36E+00
0.006	41	78	1.05E+00	1001	2.13E+01	4.22E+00
0.006	76	74	1.11E+00	1001	1.98E+01	5.85E+00
0.006	86	76	1.10E+00	1001	2.09E+01	6.58E+00
0.006	55	72	1.05E+00	1001	2.39E+01	4.89E+00
0.006	83	77	1.10E+00	1001	1.94E+01	6.31E+00
0.006	82	74	1.08E+00	1001	2.11E+01	6.45E+00
0.006	83	72	1.09E+00	1001	2.10E+01	6.36E+00
0.006	43	77	1.06E+00	1001	2.09E+01	4.25E+00
0.006	87	79	1.12E+00	1001	1.87E+01	6.55E+00

0.006	88	79	1.11E+00	1001	1.83E+01	6.65E+00
0.006	26	77	1.03E+00	1001	2.20E+01	3.72E+00
0.006	88	80	1.13E+00	1001	1.80E+01	6.53E+00
0.006	55	75	1.07E+00	1001	2.20E+01	4.74E+00
0.006	34	76	1.04E+00	1001	2.39E+01	4.03E+00
0.006	14	77	1.02E+00	1001	2.11E+01	3.40E+00
0.006	54	76	1.08E+00	1001	2.05E+01	4.69E+00
0.006	79	75	1.09E+00	1001	2.04E+01	6.10E+00
0.006	31	77	1.05E+00	1001	2.06E+01	3.79E+00
0.008	62	75	1.06E+00	1001	2.12E+01	5.21E+00
0.008	82	78	1.12E+00	1001	1.65E+01	6.05E+00
0.008	66	78	1.07E+00	1001	1.97E+01	5.35E+00
0.008	79	77	1.09E+00	1001	1.87E+01	6.01E+00
0.008	32	76	1.05E+00	1001	1.76E+01	3.80E+00
0.008	88	78	1.17E+00	1001	1.62E+01	6.40E+00
0.008	84	77	1.13E+00	1001	1.79E+01	6.25E+00
0.008	86	74	1.12E+00	1001	1.79E+01	6.42E+00
0.008	78	77	1.13E+00	1001	1.71E+01	5.80E+00
0.008	57	73	1.07E+00	1001	2.03E+01	4.91E+00
0.008	87	78	1.18E+00	1001	1.57E+01	6.05E+00
0.008	52	78	1.06E+00	1001	1.91E+01	4.67E+00
0.008	84	80	1.14E+00	1001	1.67E+01	6.07E+00
0.008	81	77	1.15E+00	1001	1.59E+01	5.83E+00
0.008	81	76	1.10E+00	1001	1.76E+01	6.16E+00
0.008	75	72	1.09E+00	1001	1.96E+01	5.77E+00
0.008	86	78	1.16E+00	1001	1.54E+01	6.05E+00
0.008	77	78	1.09E+00	1001	1.83E+01	6.00E+00
0.008	84	79	1.12E+00	1001	1.75E+01	6.26E+00
0.008	87	77	1.14E+00	1001	1.81E+01	6.45E+00
0.010	88	78	1.22E+00	1001	1.28E+01	5.83E+00
0.010	80	76	1.14E+00	1001	1.63E+01	5.79E+00
0.010	87	76	1.20E+00	1001	1.44E+01	6.05E+00
0.010	88	78	1.22E+00	1001	1.41E+01	6.06E+00
0.010	56	76	1.07E+00	1001	1.83E+01	4.79E+00
0.010	71	78	1.15E+00	1001	1.44E+01	5.11E+00
0.010	81	75	1.16E+00	1001	1.53E+01	5.73E+00
0.010	87	74	1.19E+00	1001	1.55E+01	6.10E+00
0.010	49	73	1.07E+00	1001	1.73E+01	4.43E+00
0.010	67	78	1.11E+00	1001	1.57E+01	5.12E+00
0.010	89	76	1.20E+00	1001	1.54E+01	6.21E+00
0.010	83	74	1.13E+00	1001	1.68E+01	6.04E+00
0.010	84	74	1.16E+00	1001	1.52E+01	6.07E+00
0.010	82	76	1.14E+00	1001	1.57E+01	6.06E+00
0.010	85	81	1.17E+00	1001	1.60E+01	6.10E+00
0.010	36	77	1.06E+00	1001	1.62E+01	3.89E+00
0.010	82	75	1.11E+00	1001	1.63E+01	6.13E+00
0.010	77	78	1.10E+00	1001	1.71E+01	5.84E+00
0.010	83	77	1.20E+00	1001	1.35E+01	5.67E+00
0.010	58	76	1.10E+00	1001	1.60E+01	4.69E+00
0.012	80	78	1.15E+00	1001	1.52E+01	5.71E+00
0.012	85	79	1.19E+00	1001	1.37E+01	5.83E+00
0.012	69	79	1.13E+00	1001	1.50E+01	5.12E+00
0.012	78	79	1.12E+00	1001	1.48E+01	5.67E+00
0.012	88	79	1.23E+00	1001	1.29E+01	5.87E+00
0.012	82	77	1.21E+00	1001	1.33E+01	5.55E+00
0.012	83	74	1.16E+00	1001	1.38E+01	5.82E+00
0.012	87	80	1.25E+00	1001	1.23E+01	5.76E+00
0.012	82	78	1.20E+00	1001	1.37E+01	5.57E+00

0.012	83	81	1.19E+00	1001	1.32E+01	5.59E+00
0.012	84	79	1.21E+00	1001	1.34E+01	5.62E+00
0.012	87	79	1.23E+00	1001	1.32E+01	5.80E+00
0.012	84	77	1.16E+00	1001	1.33E+01	5.76E+00
0.012	87	80	1.24E+00	1001	1.31E+01	5.87E+00
0.012	86	76	1.18E+00	1001	1.42E+01	6.04E+00
0.012	88	80	1.28E+00	1001	1.18E+01	5.61E+00
0.012	79	75	1.14E+00	1001	1.57E+01	5.72E+00
0.012	87	75	1.24E+00	1001	1.30E+01	5.95E+00
0.012	87	80	1.25E+00	1001	1.26E+01	5.67E+00
0.012	81	75	1.19E+00	1001	1.32E+01	5.66E+00
0.014	70	79	1.14E+00	1001	1.41E+01	5.14E+00
0.014	83	81	1.23E+00	1001	1.19E+01	5.35E+00
0.014	84	82	1.29E+00	1001	1.11E+01	5.22E+00
0.014	81	81	1.23E+00	1001	1.20E+01	5.38E+00
0.014	86	75	1.22E+00	1001	1.28E+01	5.72E+00
0.014	85	79	1.25E+00	1001	1.23E+01	5.71E+00
0.014	78	78	1.20E+00	1001	1.35E+01	5.41E+00
0.014	86	77	1.23E+00	1001	1.29E+01	5.79E+00
0.014	91	80	1.36E+00	1001	1.16E+01	5.43E+00
0.014	85	77	1.24E+00	1001	1.23E+01	5.61E+00
0.014	34	76	1.07E+00	1001	1.47E+01	3.80E+00
0.014	85	76	1.24E+00	1001	1.31E+01	5.68E+00
0.014	85	78	1.23E+00	1001	1.26E+01	5.59E+00
0.014	89	81	1.33E+00	1001	1.11E+01	5.45E+00
0.014	81	73	1.18E+00	1001	1.39E+01	5.68E+00
0.014	84	81	1.24E+00	1001	1.22E+01	5.57E+00
0.014	83	79	1.26E+00	1001	1.13E+01	5.28E+00
0.014	85	81	1.25E+00	1001	1.18E+01	5.45E+00
0.014	80	76	1.16E+00	1001	1.35E+01	5.57E+00
0.014	79	80	1.21E+00	1001	1.20E+01	5.20E+00
0.016	86	78	1.30E+00	1001	1.07E+01	5.30E+00
0.016	78	74	1.21E+00	1001	1.27E+01	5.26E+00
0.016	78	74	1.17E+00	1001	1.38E+01	5.54E+00
0.016	74	74	1.16E+00	1001	1.42E+01	5.34E+00
0.016	42	78	1.11E+00	1001	1.26E+01	3.90E+00
0.016	64	77	1.13E+00	1001	1.35E+01	4.73E+00
0.016	80	71	1.20E+00	1001	1.30E+01	5.54E+00
0.016	81	80	1.28E+00	1001	1.01E+01	4.95E+00
0.016	65	77	1.21E+00	1001	1.17E+01	4.47E+00
0.016	82	75	1.25E+00	1001	1.16E+01	5.29E+00
0.016	81	78	1.21E+00	1001	1.26E+01	5.51E+00
0.016	89	80	1.34E+00	1001	1.02E+01	5.18E+00
0.016	82	81	1.30E+00	1001	1.01E+01	4.83E+00
0.016	87	79	1.29E+00	1001	1.13E+01	5.45E+00
0.016	84	80	1.24E+00	1001	1.12E+01	5.30E+00
0.016	85	76	1.33E+00	1001	1.08E+01	5.14E+00
0.016	21	79	1.07E+00	1001	1.18E+01	3.32E+00
0.016	85	79	1.27E+00	1001	1.17E+01	5.42E+00
0.016	82	76	1.20E+00	1001	1.27E+01	5.59E+00
0.016	87	77	1.30E+00	1001	1.11E+01	5.41E+00
0.018	83	79	1.27E+00	1001	1.02E+01	5.01E+00
0.018	82	77	1.28E+00	1001	1.03E+01	5.01E+00
0.018	82	74	1.29E+00	1001	1.10E+01	5.13E+00
0.018	83	76	1.26E+00	1001	1.11E+01	5.29E+00
0.018	79	78	1.26E+00	1001	1.13E+01	5.15E+00
0.018	82	79	1.29E+00	1001	1.01E+01	5.01E+00
0.018	70	75	1.24E+00	1001	1.03E+01	4.55E+00

0.018	85	78	1.32E+00	1001	1.06E+01	5.20E+00
0.018	86	82	1.39E+00	1001	9.31E+00	4.80E+00
0.018	87	80	1.32E+00	1001	1.07E+01	5.33E+00
0.018	80	77	1.29E+00	1001	1.07E+01	4.96E+00
0.018	76	75	1.19E+00	1001	1.20E+01	5.10E+00
0.018	51	76	1.12E+00	1001	1.33E+01	4.26E+00
0.018	80	73	1.23E+00	1001	1.15E+01	5.18E+00
0.018	83	81	1.29E+00	1001	1.02E+01	5.00E+00
0.018	83	82	1.30E+00	1001	1.05E+01	5.06E+00
0.018	69	76	1.17E+00	1001	1.19E+01	4.80E+00
0.018	85	74	1.26E+00	1001	1.11E+01	5.38E+00
0.018	79	80	1.26E+00	1001	1.06E+01	5.00E+00
0.018	77	77	1.17E+00	1001	1.30E+01	5.38E+00
0.020	85	81	1.36E+00	1001	9.12E+00	4.85E+00
0.020	84	78	1.29E+00	1001	1.07E+01	5.22E+00
0.020	75	77	1.24E+00	1001	1.13E+01	4.91E+00
0.020	73	75	1.23E+00	1001	1.05E+01	4.81E+00
0.020	90	81	1.44E+00	1001	9.27E+00	4.93E+00
0.020	86	76	1.37E+00	1001	9.68E+00	4.94E+00
0.020	82	74	1.29E+00	1001	1.05E+01	5.10E+00
0.020	84	77	1.31E+00	1001	1.05E+01	5.09E+00
0.020	84	80	1.35E+00	1001	9.37E+00	4.90E+00
0.020	82	77	1.31E+00	1001	9.90E+00	4.95E+00
0.020	85	78	1.41E+00	1001	9.69E+00	4.79E+00
0.020	87	75	1.39E+00	1001	1.00E+01	5.04E+00
0.020	84	77	1.35E+00	1001	9.96E+00	4.95E+00
0.020	82	78	1.29E+00	1001	1.09E+01	5.10E+00
0.020	87	78	1.36E+00	1001	1.02E+01	5.17E+00
0.020	78	76	1.22E+00	1001	1.09E+01	5.09E+00
0.020	87	81	1.35E+00	1001	1.02E+01	5.09E+00
0.020	78	78	1.25E+00	1001	1.05E+01	5.01E+00
0.020	81	78	1.30E+00	1001	9.44E+00	4.95E+00
0.020	79	79	1.26E+00	1001	1.10E+01	4.92E+00

Experiment 5.5.2

Movement probability	Average cooperation	Average relatedness	Average interaction length	Model time	Average cell population	Average number of partners
0.0	24	84	0.00E+00	1001	6.94E+01	0.00E+00
0.0	47	84	0.00E+00	1001	5.45E+01	0.00E+00
0.0	33	85	0.00E+00	1001	7.03E+01	0.00E+00
0.0	25	84	0.00E+00	1001	6.88E+01	0.00E+00
0.0	25	82	0.00E+00	1001	6.95E+01	0.00E+00
0.0	34	78	0.00E+00	1001	6.76E+01	0.00E+00
0.0	30	83	0.00E+00	1001	7.58E+01	0.00E+00
0.0	27	84	0.00E+00	1001	6.59E+01	0.00E+00
0.0	33	84	0.00E+00	1001	6.11E+01	0.00E+00
0.0	28	84	0.00E+00	1001	6.00E+01	0.00E+00
0.0	17	83	0.00E+00	1001	8.23E+01	0.00E+00
0.0	26	83	0.00E+00	1001	6.57E+01	0.00E+00
0.0	24	84	0.00E+00	1001	7.64E+01	0.00E+00
0.0	24	84	0.00E+00	1001	7.07E+01	0.00E+00
0.0	21	83	0.00E+00	1001	6.78E+01	0.00E+00
0.0	29	83	0.00E+00	1001	5.47E+01	0.00E+00
0.0	16	84	0.00E+00	1001	7.15E+01	0.00E+00
0.0	27	82	0.00E+00	1001	6.79E+01	0.00E+00
0.0	13	84	0.00E+00	1001	8.70E+01	0.00E+00
0.0	20	85	0.00E+00	1001	6.66E+01	0.00E+00
0.1	48	80	0.00E+00	1001	4.52E+00	0.00E+00

0.1	43	76	0.00E+00	1001	4.49E+00	0.00E+00
0.1	35	79	0.00E+00	1001	4.80E+00	0.00E+00
0.1	41	76	0.00E+00	1001	4.65E+00	0.00E+00
0.1	37	80	0.00E+00	1001	4.63E+00	0.00E+00
0.1	33	75	0.00E+00	1001	4.83E+00	0.00E+00
0.1	37	78	0.00E+00	1001	4.66E+00	0.00E+00
0.1	39	78	0.00E+00	1001	4.48E+00	0.00E+00
0.1	31	73	0.00E+00	1001	4.73E+00	0.00E+00
0.1	37	74	0.00E+00	1001	4.71E+00	0.00E+00
0.1	41	80	0.00E+00	1001	4.51E+00	0.00E+00
0.1	39	81	0.00E+00	1001	4.49E+00	0.00E+00
0.1	34	72	0.00E+00	1001	4.64E+00	0.00E+00
0.1	34	79	0.00E+00	1001	4.77E+00	0.00E+00
0.1	40	78	0.00E+00	1001	4.53E+00	0.00E+00
0.1	38	74	0.00E+00	1001	4.62E+00	0.00E+00
0.1	35	80	0.00E+00	1001	4.81E+00	0.00E+00
0.1	38	78	0.00E+00	1001	4.71E+00	0.00E+00
0.1	31	75	0.00E+00	1001	4.60E+00	0.00E+00
0.1	47	76	0.00E+00	1001	4.42E+00	0.00E+00
0.2	21	77	0.00E+00	1001	3.37E+00	0.00E+00
0.2	22	77	0.00E+00	1001	3.39E+00	0.00E+00
0.2	22	77	0.00E+00	1001	3.39E+00	0.00E+00
0.2	22	76	0.00E+00	1001	3.55E+00	0.00E+00
0.2	27	76	0.00E+00	1001	3.39E+00	0.00E+00
0.2	24	76	0.00E+00	1001	3.38E+00	0.00E+00
0.2	23	77	0.00E+00	1001	3.43E+00	0.00E+00
0.2	26	76	0.00E+00	1001	3.39E+00	0.00E+00
0.2	17	80	0.00E+00	1001	3.50E+00	0.00E+00
0.2	25	76	0.00E+00	1001	3.50E+00	0.00E+00
0.2	17	78	0.00E+00	1001	3.50E+00	0.00E+00
0.2	23	75	0.00E+00	1001	3.42E+00	0.00E+00
0.2	19	76	0.00E+00	1001	3.54E+00	0.00E+00
0.2	27	74	0.00E+00	1001	3.46E+00	0.00E+00
0.2	20	77	0.00E+00	1001	3.43E+00	0.00E+00
0.2	25	79	0.00E+00	1001	3.25E+00	0.00E+00
0.2	23	76	0.00E+00	1001	3.41E+00	0.00E+00
0.2	30	76	0.00E+00	1001	3.32E+00	0.00E+00
0.2	23	77	0.00E+00	1001	3.41E+00	0.00E+00
0.2	15	82	0.00E+00	1001	3.34E+00	0.00E+00
0.3	17	78	0.00E+00	1001	2.85E+00	0.00E+00
0.3	16	80	0.00E+00	1001	2.86E+00	0.00E+00
0.3	15	80	0.00E+00	1001	2.93E+00	0.00E+00
0.3	26	81	0.00E+00	1001	2.82E+00	0.00E+00
0.3	13	82	0.00E+00	1001	2.95E+00	0.00E+00
0.3	17	79	0.00E+00	1001	2.84E+00	0.00E+00
0.3	14	81	0.00E+00	1001	2.88E+00	0.00E+00
0.3	12	83	0.00E+00	1001	2.86E+00	0.00E+00
0.3	11	83	0.00E+00	1001	2.90E+00	0.00E+00
0.3	11	83	0.00E+00	1001	2.84E+00	0.00E+00
0.3	9	85	0.00E+00	1001	2.84E+00	0.00E+00
0.3	11	82	0.00E+00	1001	2.99E+00	0.00E+00
0.3	12	82	0.00E+00	1001	2.99E+00	0.00E+00
0.3	15	80	0.00E+00	1001	2.88E+00	0.00E+00
0.3	17	78	0.00E+00	1001	2.88E+00	0.00E+00
0.3	15	80	0.00E+00	1001	2.82E+00	0.00E+00
0.3	20	76	0.00E+00	1001	2.81E+00	0.00E+00
0.3	19	80	0.00E+00	1001	2.91E+00	0.00E+00
0.3	14	82	0.00E+00	1001	2.89E+00	0.00E+00

0.3	14	79	0.00E+00	1001	2.91E+00	0.00E+00
0.4	16	79	0.00E+00	1001	2.50E+00	0.00E+00
0.4	22	75	0.00E+00	1001	2.53E+00	0.00E+00
0.4	12	81	0.00E+00	1001	2.56E+00	0.00E+00
0.4	9	85	0.00E+00	1001	2.57E+00	0.00E+00
0.4	12	81	0.00E+00	1001	2.54E+00	0.00E+00
0.4	11	82	0.00E+00	1001	2.54E+00	0.00E+00
0.4	9	84	0.00E+00	1001	2.57E+00	0.00E+00
0.4	18	75	0.00E+00	1001	2.51E+00	0.00E+00
0.4	12	81	0.00E+00	1001	2.54E+00	0.00E+00
0.4	11	83	0.00E+00	1001	2.51E+00	0.00E+00
0.4	11	82	0.00E+00	1001	2.61E+00	0.00E+00
0.4	12	81	0.00E+00	1001	2.52E+00	0.00E+00
0.4	11	87	0.00E+00	1001	2.56E+00	0.00E+00
0.4	10	83	0.00E+00	1001	2.51E+00	0.00E+00
0.4	13	80	0.00E+00	1001	2.51E+00	0.00E+00
0.4	14	82	0.00E+00	1001	2.47E+00	0.00E+00
0.4	12	80	0.00E+00	1001	2.48E+00	0.00E+00
0.4	16	80	0.00E+00	1001	2.51E+00	0.00E+00
0.4	14	80	0.00E+00	1001	2.51E+00	0.00E+00
0.4	15	80	0.00E+00	1001	2.58E+00	0.00E+00
0.5	9	85	0.00E+00	1001	2.31E+00	0.00E+00
0.5	13	80	0.00E+00	1001	2.32E+00	0.00E+00
0.5	10	83	0.00E+00	1001	2.36E+00	0.00E+00
0.5	12	82	0.00E+00	1001	2.32E+00	0.00E+00
0.5	8	87	0.00E+00	1001	2.30E+00	0.00E+00
0.5	11	82	0.00E+00	1001	2.26E+00	0.00E+00
0.5	9	84	0.00E+00	1001	2.32E+00	0.00E+00
0.5	10	83	0.00E+00	1001	2.30E+00	0.00E+00
0.5	9	84	0.00E+00	1001	2.31E+00	0.00E+00
0.5	9	85	0.00E+00	1001	2.32E+00	0.00E+00
0.5	10	83	0.00E+00	1001	2.29E+00	0.00E+00
0.5	11	81	0.00E+00	1001	2.30E+00	0.00E+00
0.5	10	83	0.00E+00	1001	2.34E+00	0.00E+00
0.5	13	80	0.00E+00	1001	2.30E+00	0.00E+00
0.5	11	82	0.00E+00	1001	2.30E+00	0.00E+00
0.5	10	84	0.00E+00	1001	2.30E+00	0.00E+00
0.5	8	85	0.00E+00	1001	2.31E+00	0.00E+00
0.5	9	84	0.00E+00	1001	2.37E+00	0.00E+00
0.5	10	84	0.00E+00	1001	2.30E+00	0.00E+00
0.5	11	82	0.00E+00	1001	2.35E+00	0.00E+00
0.6	11	81	0.00E+00	1001	2.16E+00	0.00E+00
0.6	8	86	0.00E+00	1001	2.20E+00	0.00E+00
0.6	9	84	0.00E+00	1001	2.17E+00	0.00E+00
0.6	7	86	0.00E+00	1001	2.17E+00	0.00E+00
0.6	11	81	0.00E+00	1001	2.16E+00	0.00E+00
0.6	12	82	0.00E+00	1001	2.17E+00	0.00E+00
0.6	9	84	0.00E+00	1001	2.15E+00	0.00E+00
0.6	9	84	0.00E+00	1001	2.17E+00	0.00E+00
0.6	10	83	0.00E+00	1001	2.15E+00	0.00E+00
0.6	8	85	0.00E+00	1001	2.18E+00	0.00E+00
0.6	7	87	0.00E+00	1001	2.17E+00	0.00E+00
0.6	12	81	0.00E+00	1001	2.17E+00	0.00E+00
0.6	9	84	0.00E+00	1001	2.15E+00	0.00E+00
0.6	10	83	0.00E+00	1001	2.18E+00	0.00E+00
0.6	13	80	0.00E+00	1001	2.14E+00	0.00E+00
0.6	10	83	0.00E+00	1001	2.18E+00	0.00E+00
0.6	10	84	0.00E+00	1001	2.16E+00	0.00E+00

0.6	9	83	0.00E+00	1001	2.16E+00	0.00E+00
0.6	10	84	0.00E+00	1001	2.17E+00	0.00E+00
0.6	11	81	0.00E+00	1001	2.19E+00	0.00E+00
0.7	10	83	0.00E+00	1001	2.06E+00	0.00E+00
0.7	10	83	0.00E+00	1001	2.05E+00	0.00E+00
0.7	8	86	0.00E+00	1001	2.07E+00	0.00E+00
0.7	8	85	0.00E+00	1001	2.03E+00	0.00E+00
0.7	11	81	0.00E+00	1001	2.06E+00	0.00E+00
0.7	8	85	0.00E+00	1001	2.07E+00	0.00E+00
0.7	7	86	0.00E+00	1001	2.03E+00	0.00E+00
0.7	12	79	0.00E+00	1001	2.05E+00	0.00E+00
0.7	8	86	0.00E+00	1001	2.04E+00	0.00E+00
0.7	8	85	0.00E+00	1001	2.04E+00	0.00E+00
0.7	10	82	0.00E+00	1001	2.06E+00	0.00E+00
0.7	10	83	0.00E+00	1001	2.05E+00	0.00E+00
0.7	9	84	0.00E+00	1001	2.04E+00	0.00E+00
0.7	9	83	0.00E+00	1001	2.08E+00	0.00E+00
0.7	8	85	0.00E+00	1001	2.07E+00	0.00E+00
0.7	10	83	0.00E+00	1001	2.06E+00	0.00E+00
0.7	9	84	0.00E+00	1001	2.07E+00	0.00E+00
0.7	9	84	0.00E+00	1001	2.04E+00	0.00E+00
0.7	6	87	0.00E+00	1001	2.03E+00	0.00E+00
0.7	9	83	0.00E+00	1001	2.05E+00	0.00E+00
0.8	8	84	0.00E+00	1001	1.93E+00	0.00E+00
0.8	8	86	0.00E+00	1001	1.96E+00	0.00E+00
0.8	11	82	0.00E+00	1001	1.97E+00	0.00E+00
0.8	7	86	0.00E+00	1001	1.98E+00	0.00E+00
0.8	12	81	0.00E+00	1001	1.99E+00	0.00E+00
0.8	8	85	0.00E+00	1001	1.96E+00	0.00E+00
0.8	8	85	0.00E+00	1001	1.96E+00	0.00E+00
0.8	7	87	0.00E+00	1001	1.97E+00	0.00E+00
0.8	10	84	0.00E+00	1001	1.98E+00	0.00E+00
0.8	8	85	0.00E+00	1001	2.01E+00	0.00E+00
0.8	7	86	0.00E+00	1001	2.00E+00	0.00E+00
0.8	8	85	0.00E+00	1001	1.97E+00	0.00E+00
0.8	11	81	0.00E+00	1001	1.98E+00	0.00E+00
0.8	10	82	0.00E+00	1001	1.98E+00	0.00E+00
0.8	8	85	0.00E+00	1001	1.96E+00	0.00E+00
0.8	8	85	0.00E+00	1001	2.00E+00	0.00E+00
0.8	7	86	0.00E+00	1001	1.97E+00	0.00E+00
0.8	7	85	0.00E+00	1001	1.97E+00	0.00E+00
0.8	9	83	0.00E+00	1001	1.97E+00	0.00E+00
0.8	8	85	0.00E+00	1001	1.97E+00	0.00E+00
0.9	8	85	0.00E+00	1001	1.92E+00	0.00E+00
0.9	8	86	0.00E+00	1001	1.92E+00	0.00E+00
0.9	10	82	0.00E+00	1001	1.94E+00	0.00E+00
0.9	7	86	0.00E+00	1001	1.93E+00	0.00E+00
0.9	9	84	0.00E+00	1001	1.92E+00	0.00E+00
0.9	7	86	0.00E+00	1001	1.94E+00	0.00E+00
0.9	9	84	0.00E+00	1001	1.94E+00	0.00E+00
0.9	7	85	0.00E+00	1001	1.90E+00	0.00E+00
0.9	8	85	0.00E+00	1001	1.93E+00	0.00E+00
0.9	8	84	0.00E+00	1001	1.93E+00	0.00E+00
0.9	8	84	0.00E+00	1001	1.93E+00	0.00E+00
0.9	9	84	0.00E+00	1001	1.93E+00	0.00E+00
0.9	7	86	0.00E+00	1001	1.94E+00	0.00E+00
0.9	8	85	0.00E+00	1001	1.94E+00	0.00E+00
0.9	7	86	0.00E+00	1001	1.92E+00	0.00E+00

0.9	8	84	0.00E+00	1001	1.92E+00	0.00E+00
0.9	8	85	0.00E+00	1001	1.92E+00	0.00E+00
0.9	6	87	0.00E+00	1001	1.91E+00	0.00E+00
0.9	9	84	0.00E+00	1001	1.93E+00	0.00E+00
0.9	7	87	0.00E+00	1001	1.92E+00	0.00E+00
1.0	8	85	0.00E+00	1001	1.88E+00	0.00E+00
1.0	8	84	0.00E+00	1001	1.90E+00	0.00E+00
1.0	5	88	0.00E+00	1001	1.88E+00	0.00E+00
1.0	7	87	0.00E+00	1001	1.90E+00	0.00E+00
1.0	9	84	0.00E+00	1001	1.88E+00	0.00E+00
1.0	7	85	0.00E+00	1001	1.90E+00	0.00E+00
1.0	7	86	0.00E+00	1001	1.88E+00	0.00E+00
1.0	6	88	0.00E+00	1001	1.88E+00	0.00E+00
1.0	9	83	0.00E+00	1001	1.89E+00	0.00E+00
1.0	7	86	0.00E+00	1001	1.88E+00	0.00E+00
1.0	8	85	0.00E+00	1001	1.89E+00	0.00E+00
1.0	7	87	0.00E+00	1001	1.88E+00	0.00E+00
1.0	6	88	0.00E+00	1001	1.87E+00	0.00E+00
1.0	8	85	0.00E+00	1001	1.90E+00	0.00E+00
1.0	6	87	0.00E+00	1001	1.88E+00	0.00E+00
1.0	9	83	0.00E+00	1001	1.89E+00	0.00E+00
1.0	6	88	0.00E+00	1001	1.87E+00	0.00E+00
1.0	7	86	0.00E+00	1001	1.89E+00	0.00E+00
1.0	7	87	0.00E+00	1001	1.88E+00	0.00E+00
1.0	11	81	0.00E+00	1001	1.90E+00	0.00E+00

Experiment 5.5.3

Movement probability	Average cooperation	Average relatedness	Average interaction length	Model time	Average cell population	Average number of partners
0.00	24	84	0.00E+00	1001	6.94E+01	0.00E+00
0.00	47	84	0.00E+00	1001	5.45E+01	0.00E+00
0.00	33	85	0.00E+00	1001	7.03E+01	0.00E+00
0.00	25	84	0.00E+00	1001	6.88E+01	0.00E+00
0.00	25	82	0.00E+00	1001	6.95E+01	0.00E+00
0.00	34	78	0.00E+00	1001	6.76E+01	0.00E+00
0.00	30	83	0.00E+00	1001	7.58E+01	0.00E+00
0.00	27	84	0.00E+00	1001	6.59E+01	0.00E+00
0.00	33	84	0.00E+00	1001	6.11E+01	0.00E+00
0.00	28	84	0.00E+00	1001	6.00E+01	0.00E+00
0.00	17	83	0.00E+00	1001	8.23E+01	0.00E+00
0.00	26	83	0.00E+00	1001	6.57E+01	0.00E+00
0.00	24	84	0.00E+00	1001	7.64E+01	0.00E+00
0.00	24	84	0.00E+00	1001	7.07E+01	0.00E+00
0.00	21	83	0.00E+00	1001	6.78E+01	0.00E+00
0.00	29	83	0.00E+00	1001	5.47E+01	0.00E+00
0.00	16	84	0.00E+00	1001	7.15E+01	0.00E+00
0.00	27	82	0.00E+00	1001	6.79E+01	0.00E+00
0.00	13	84	0.00E+00	1001	8.70E+01	0.00E+00
0.00	20	85	0.00E+00	1001	6.66E+01	0.00E+00
0.02	70	85	0.00E+00	1001	8.65E+00	0.00E+00
0.02	54	80	0.00E+00	1001	1.07E+01	0.00E+00
0.02	72	82	0.00E+00	1001	9.76E+00	0.00E+00
0.02	69	82	0.00E+00	1001	1.02E+01	0.00E+00
0.02	52	80	0.00E+00	1001	1.07E+01	0.00E+00
0.02	60	80	0.00E+00	1001	1.09E+01	0.00E+00
0.02	85	87	0.00E+00	1001	8.36E+00	0.00E+00
0.02	78	84	0.00E+00	1001	9.47E+00	0.00E+00
0.02	61	86	0.00E+00	1001	9.33E+00	0.00E+00

0.02	54	80	0.00E+00	1001	1.01E+01	0.00E+00
0.02	46	83	0.00E+00	1001	1.04E+01	0.00E+00
0.02	51	83	0.00E+00	1001	9.69E+00	0.00E+00
0.02	76	82	0.00E+00	1001	9.22E+00	0.00E+00
0.02	75	83	0.00E+00	1001	9.77E+00	0.00E+00
0.02	69	85	0.00E+00	1001	9.88E+00	0.00E+00
0.02	49	83	0.00E+00	1001	9.69E+00	0.00E+00
0.02	49	84	0.00E+00	1001	9.89E+00	0.00E+00
0.02	48	84	0.00E+00	1001	9.04E+00	0.00E+00
0.02	54	79	0.00E+00	1001	9.61E+00	0.00E+00
0.02	80	85	0.00E+00	1001	8.62E+00	0.00E+00
0.04	49	79	0.00E+00	1001	6.75E+00	0.00E+00
0.04	52	81	0.00E+00	1001	6.91E+00	0.00E+00
0.04	54	78	0.00E+00	1001	6.79E+00	0.00E+00
0.04	74	83	0.00E+00	1001	6.70E+00	0.00E+00
0.04	48	86	0.00E+00	1001	6.79E+00	0.00E+00
0.04	65	75	0.00E+00	1001	7.29E+00	0.00E+00
0.04	57	81	0.00E+00	1001	6.85E+00	0.00E+00
0.04	50	80	0.00E+00	1001	7.10E+00	0.00E+00
0.04	67	76	0.00E+00	1001	7.06E+00	0.00E+00
0.04	52	80	0.00E+00	1001	7.45E+00	0.00E+00
0.04	66	80	0.00E+00	1001	6.77E+00	0.00E+00
0.04	66	76	0.00E+00	1001	7.18E+00	0.00E+00
0.04	55	84	0.00E+00	1001	7.08E+00	0.00E+00
0.04	67	77	0.00E+00	1001	7.22E+00	0.00E+00
0.04	61	77	0.00E+00	1001	6.86E+00	0.00E+00
0.04	59	79	0.00E+00	1001	7.11E+00	0.00E+00
0.04	48	77	0.00E+00	1001	6.74E+00	0.00E+00
0.04	55	79	0.00E+00	1001	7.19E+00	0.00E+00
0.04	46	80	0.00E+00	1001	6.57E+00	0.00E+00
0.04	48	79	0.00E+00	1001	7.20E+00	0.00E+00
0.06	57	85	0.00E+00	1001	5.59E+00	0.00E+00
0.06	72	77	0.00E+00	1001	5.33E+00	0.00E+00
0.06	45	77	0.00E+00	1001	5.96E+00	0.00E+00
0.06	39	81	0.00E+00	1001	5.86E+00	0.00E+00
0.06	51	79	0.00E+00	1001	5.35E+00	0.00E+00
0.06	46	81	0.00E+00	1001	6.05E+00	0.00E+00
0.06	40	82	0.00E+00	1001	5.65E+00	0.00E+00
0.06	40	77	0.00E+00	1001	5.60E+00	0.00E+00
0.06	51	81	0.00E+00	1001	5.62E+00	0.00E+00
0.06	49	83	0.00E+00	1001	5.73E+00	0.00E+00
0.06	42	82	0.00E+00	1001	5.57E+00	0.00E+00
0.06	40	77	0.00E+00	1001	5.88E+00	0.00E+00
0.06	53	82	0.00E+00	1001	5.53E+00	0.00E+00
0.06	53	77	0.00E+00	1001	5.33E+00	0.00E+00
0.06	38	80	0.00E+00	1001	5.93E+00	0.00E+00
0.06	44	77	0.00E+00	1001	5.48E+00	0.00E+00
0.06	51	76	0.00E+00	1001	5.74E+00	0.00E+00
0.06	47	81	0.00E+00	1001	5.77E+00	0.00E+00
0.06	60	75	0.00E+00	1001	5.55E+00	0.00E+00
0.06	58	78	0.00E+00	1001	5.38E+00	0.00E+00
0.08	64	73	0.00E+00	1001	4.89E+00	0.00E+00
0.08	52	83	0.00E+00	1001	5.08E+00	0.00E+00
0.08	51	81	0.00E+00	1001	4.82E+00	0.00E+00
0.08	42	75	0.00E+00	1001	4.80E+00	0.00E+00
0.08	46	80	0.00E+00	1001	5.05E+00	0.00E+00
0.08	52	84	0.00E+00	1001	4.88E+00	0.00E+00
0.08	43	73	0.00E+00	1001	4.83E+00	0.00E+00

0.08	45	78	0.00E+00	1001	5.19E+00	0.00E+00
0.08	42	79	0.00E+00	1001	5.21E+00	0.00E+00
0.08	36	79	0.00E+00	1001	5.09E+00	0.00E+00
0.08	53	78	0.00E+00	1001	4.78E+00	0.00E+00
0.08	52	79	0.00E+00	1001	4.73E+00	0.00E+00
0.08	39	79	0.00E+00	1001	5.01E+00	0.00E+00
0.08	43	78	0.00E+00	1001	4.98E+00	0.00E+00
0.08	43	76	0.00E+00	1001	5.03E+00	0.00E+00
0.08	48	79	0.00E+00	1001	4.83E+00	0.00E+00
0.08	46	76	0.00E+00	1001	5.10E+00	0.00E+00
0.08	49	82	0.00E+00	1001	4.97E+00	0.00E+00
0.08	45	78	0.00E+00	1001	4.98E+00	0.00E+00
0.08	41	83	0.00E+00	1001	5.03E+00	0.00E+00
0.10	43	76	0.00E+00	1001	4.50E+00	0.00E+00
0.10	62	75	0.00E+00	1001	4.47E+00	0.00E+00
0.10	41	77	0.00E+00	1001	4.57E+00	0.00E+00
0.10	32	79	0.00E+00	1001	4.69E+00	0.00E+00
0.10	44	81	0.00E+00	1001	4.54E+00	0.00E+00
0.10	42	76	0.00E+00	1001	4.40E+00	0.00E+00
0.10	35	77	0.00E+00	1001	4.63E+00	0.00E+00
0.10	38	81	0.00E+00	1001	4.69E+00	0.00E+00
0.10	37	79	0.00E+00	1001	4.44E+00	0.00E+00
0.10	37	79	0.00E+00	1001	4.53E+00	0.00E+00
0.10	35	72	0.00E+00	1001	4.51E+00	0.00E+00
0.10	40	81	0.00E+00	1001	4.30E+00	0.00E+00
0.10	46	76	0.00E+00	1001	4.45E+00	0.00E+00
0.10	40	82	0.00E+00	1001	4.48E+00	0.00E+00
0.10	39	79	0.00E+00	1001	4.26E+00	0.00E+00
0.10	38	72	0.00E+00	1001	4.67E+00	0.00E+00
0.10	30	77	0.00E+00	1001	4.66E+00	0.00E+00
0.10	33	78	0.00E+00	1001	4.49E+00	0.00E+00
0.10	35	80	0.00E+00	1001	4.47E+00	0.00E+00
0.10	36	79	0.00E+00	1001	4.58E+00	0.00E+00
0.12	32	74	0.00E+00	1001	4.22E+00	0.00E+00
0.12	35	74	0.00E+00	1001	4.15E+00	0.00E+00
0.12	25	75	0.00E+00	1001	4.44E+00	0.00E+00
0.12	44	80	0.00E+00	1001	4.17E+00	0.00E+00
0.12	38	76	0.00E+00	1001	4.13E+00	0.00E+00
0.12	33	75	0.00E+00	1001	4.26E+00	0.00E+00
0.12	38	77	0.00E+00	1001	4.13E+00	0.00E+00
0.12	37	76	0.00E+00	1001	4.23E+00	0.00E+00
0.12	36	73	0.00E+00	1001	4.17E+00	0.00E+00
0.12	29	74	0.00E+00	1001	4.37E+00	0.00E+00
0.12	33	77	0.00E+00	1001	4.19E+00	0.00E+00
0.12	33	73	0.00E+00	1001	4.26E+00	0.00E+00
0.12	41	81	0.00E+00	1001	4.10E+00	0.00E+00
0.12	22	82	0.00E+00	1001	4.30E+00	0.00E+00
0.12	39	74	0.00E+00	1001	4.21E+00	0.00E+00
0.12	36	77	0.00E+00	1001	4.28E+00	0.00E+00
0.12	37	78	0.00E+00	1001	4.14E+00	0.00E+00
0.12	22	77	0.00E+00	1001	4.39E+00	0.00E+00
0.12	33	75	0.00E+00	1001	4.18E+00	0.00E+00
0.12	24	76	0.00E+00	1001	4.32E+00	0.00E+00
0.14	29	74	0.00E+00	1001	4.03E+00	0.00E+00
0.14	33	75	0.00E+00	1001	4.02E+00	0.00E+00
0.14	25	75	0.00E+00	1001	3.97E+00	0.00E+00
0.14	29	77	0.00E+00	1001	3.92E+00	0.00E+00
0.14	32	75	0.00E+00	1001	3.71E+00	0.00E+00

0.14	33	78	0.00E+00	1001	3.99E+00	0.00E+00
0.14	24	77	0.00E+00	1001	3.95E+00	0.00E+00
0.14	34	75	0.00E+00	1001	3.99E+00	0.00E+00
0.14	29	75	0.00E+00	1001	3.86E+00	0.00E+00
0.14	33	76	0.00E+00	1001	4.05E+00	0.00E+00
0.14	23	77	0.00E+00	1001	4.07E+00	0.00E+00
0.14	23	76	0.00E+00	1001	4.10E+00	0.00E+00
0.14	24	75	0.00E+00	1001	3.81E+00	0.00E+00
0.14	22	77	0.00E+00	1001	4.01E+00	0.00E+00
0.14	26	77	0.00E+00	1001	3.96E+00	0.00E+00
0.14	28	77	0.00E+00	1001	4.00E+00	0.00E+00
0.14	29	77	0.00E+00	1001	4.08E+00	0.00E+00
0.14	29	77	0.00E+00	1001	3.96E+00	0.00E+00
0.14	35	74	0.00E+00	1001	3.87E+00	0.00E+00
0.14	29	74	0.00E+00	1001	3.91E+00	0.00E+00
0.16	23	77	0.00E+00	1001	3.90E+00	0.00E+00
0.16	27	76	0.00E+00	1001	3.78E+00	0.00E+00
0.16	31	78	0.00E+00	1001	3.74E+00	0.00E+00
0.16	21	77	0.00E+00	1001	3.78E+00	0.00E+00
0.16	23	77	0.00E+00	1001	3.79E+00	0.00E+00
0.16	29	77	0.00E+00	1001	3.81E+00	0.00E+00
0.16	24	74	0.00E+00	1001	3.70E+00	0.00E+00
0.16	30	73	0.00E+00	1001	3.77E+00	0.00E+00
0.16	19	79	0.00E+00	1001	3.87E+00	0.00E+00
0.16	37	77	0.00E+00	1001	3.66E+00	0.00E+00
0.16	27	74	0.00E+00	1001	3.81E+00	0.00E+00
0.16	27	74	0.00E+00	1001	3.75E+00	0.00E+00
0.16	25	74	0.00E+00	1001	3.76E+00	0.00E+00
0.16	29	74	0.00E+00	1001	3.89E+00	0.00E+00
0.16	28	73	0.00E+00	1001	3.82E+00	0.00E+00
0.16	28	74	0.00E+00	1001	3.76E+00	0.00E+00
0.16	32	75	0.00E+00	1001	3.78E+00	0.00E+00
0.16	22	75	0.00E+00	1001	4.01E+00	0.00E+00
0.16	35	77	0.00E+00	1001	3.71E+00	0.00E+00
0.16	29	72	0.00E+00	1001	3.88E+00	0.00E+00
0.18	36	78	0.00E+00	1001	3.48E+00	0.00E+00
0.18	24	74	0.00E+00	1001	3.57E+00	0.00E+00
0.18	20	76	0.00E+00	1001	3.60E+00	0.00E+00
0.18	23	74	0.00E+00	1001	3.65E+00	0.00E+00
0.18	21	78	0.00E+00	1001	3.64E+00	0.00E+00
0.18	23	75	0.00E+00	1001	3.65E+00	0.00E+00
0.18	29	75	0.00E+00	1001	3.49E+00	0.00E+00
0.18	24	77	0.00E+00	1001	3.64E+00	0.00E+00
0.18	29	76	0.00E+00	1001	3.44E+00	0.00E+00
0.18	26	74	0.00E+00	1001	3.59E+00	0.00E+00
0.18	26	78	0.00E+00	1001	3.55E+00	0.00E+00
0.18	26	78	0.00E+00	1001	3.64E+00	0.00E+00
0.18	29	74	0.00E+00	1001	3.61E+00	0.00E+00
0.18	26	75	0.00E+00	1001	3.28E+00	0.00E+00
0.18	20	76	0.00E+00	1001	3.67E+00	0.00E+00
0.18	25	74	0.00E+00	1001	3.50E+00	0.00E+00
0.18	21	78	0.00E+00	1001	3.48E+00	0.00E+00
0.18	21	76	0.00E+00	1001	3.60E+00	0.00E+00
0.18	21	80	0.00E+00	1001	3.60E+00	0.00E+00
0.18	22	79	0.00E+00	1001	3.53E+00	0.00E+00
0.20	22	77	0.00E+00	1001	3.45E+00	0.00E+00
0.20	19	77	0.00E+00	1001	3.44E+00	0.00E+00
0.20	25	76	0.00E+00	1001	3.45E+00	0.00E+00

0.20	26	73	0.00E+00	1001	3.48E+00	0.00E+00
0.20	19	77	0.00E+00	1001	3.52E+00	0.00E+00
0.20	28	75	0.00E+00	1001	3.32E+00	0.00E+00
0.20	22	75	0.00E+00	1001	3.36E+00	0.00E+00
0.20	19	78	0.00E+00	1001	3.54E+00	0.00E+00
0.20	19	77	0.00E+00	1001	3.45E+00	0.00E+00
0.20	17	81	0.00E+00	1001	3.46E+00	0.00E+00
0.20	23	76	0.00E+00	1001	3.39E+00	0.00E+00
0.20	14	80	0.00E+00	1001	3.42E+00	0.00E+00
0.20	32	74	0.00E+00	1001	3.33E+00	0.00E+00
0.20	14	80	0.00E+00	1001	3.49E+00	0.00E+00
0.20	20	78	0.00E+00	1001	3.47E+00	0.00E+00
0.20	19	76	0.00E+00	1001	3.53E+00	0.00E+00
0.20	27	75	0.00E+00	1001	3.48E+00	0.00E+00
0.20	20	76	0.00E+00	1001	3.44E+00	0.00E+00
0.20	20	77	0.00E+00	1001	3.48E+00	0.00E+00
0.20	20	75	0.00E+00	1001	3.55E+00	0.00E+00

Experiment 5.5.4

Movement probability	Average cooperation	Average relatedness	Average interaction length	Model time	Average cell population	Average number of partners
0.000	24	84	0.00E+00	1001	6.94E+01	0.00E+00
0.000	47	84	0.00E+00	1001	5.45E+01	0.00E+00
0.000	33	85	0.00E+00	1001	7.03E+01	0.00E+00
0.000	25	84	0.00E+00	1001	6.88E+01	0.00E+00
0.000	25	82	0.00E+00	1001	6.95E+01	0.00E+00
0.000	34	78	0.00E+00	1001	6.76E+01	0.00E+00
0.000	30	83	0.00E+00	1001	7.58E+01	0.00E+00
0.000	27	84	0.00E+00	1001	6.59E+01	0.00E+00
0.000	33	84	0.00E+00	1001	6.11E+01	0.00E+00
0.000	28	84	0.00E+00	1001	6.00E+01	0.00E+00
0.000	17	83	0.00E+00	1001	8.23E+01	0.00E+00
0.000	26	83	0.00E+00	1001	6.57E+01	0.00E+00
0.000	24	84	0.00E+00	1001	7.64E+01	0.00E+00
0.000	24	84	0.00E+00	1001	7.07E+01	0.00E+00
0.000	21	83	0.00E+00	1001	6.78E+01	0.00E+00
0.000	29	83	0.00E+00	1001	5.47E+01	0.00E+00
0.000	16	84	0.00E+00	1001	7.15E+01	0.00E+00
0.000	27	82	0.00E+00	1001	6.79E+01	0.00E+00
0.000	13	84	0.00E+00	1001	8.70E+01	0.00E+00
0.000	20	85	0.00E+00	1001	6.66E+01	0.00E+00
0.002	38	84	0.00E+00	1001	4.09E+01	0.00E+00
0.002	39	83	0.00E+00	1001	4.12E+01	0.00E+00
0.002	49	84	0.00E+00	1001	3.50E+01	0.00E+00
0.002	27	84	0.00E+00	1001	3.52E+01	0.00E+00
0.002	19	87	0.00E+00	1001	4.17E+01	0.00E+00
0.002	15	85	0.00E+00	1001	4.60E+01	0.00E+00
0.002	33	82	0.00E+00	1001	4.23E+01	0.00E+00
0.002	34	82	0.00E+00	1001	3.93E+01	0.00E+00
0.002	19	84	0.00E+00	1001	4.38E+01	0.00E+00
0.002	20	83	0.00E+00	1001	4.20E+01	0.00E+00
0.002	58	79	0.00E+00	1001	3.46E+01	0.00E+00
0.002	30	84	0.00E+00	1001	3.96E+01	0.00E+00
0.002	28	84	0.00E+00	1001	4.14E+01	0.00E+00
0.002	52	85	0.00E+00	1001	3.78E+01	0.00E+00
0.002	79	81	0.00E+00	1001	3.34E+01	0.00E+00
0.002	39	85	0.00E+00	1001	4.25E+01	0.00E+00
0.002	29	82	0.00E+00	1001	4.60E+01	0.00E+00

0.002	21	83	0.00E+00	1001	4.62E+01	0.00E+00
0.002	56	82	0.00E+00	1001	3.26E+01	0.00E+00
0.002	29	82	0.00E+00	1001	3.74E+01	0.00E+00
0.004	62	80	0.00E+00	1001	2.44E+01	0.00E+00
0.004	60	75	0.00E+00	1001	2.85E+01	0.00E+00
0.004	46	82	0.00E+00	1001	2.69E+01	0.00E+00
0.004	50	80	0.00E+00	1001	2.79E+01	0.00E+00
0.004	26	84	0.00E+00	1001	2.98E+01	0.00E+00
0.004	31	82	0.00E+00	1001	2.92E+01	0.00E+00
0.004	31	80	0.00E+00	1001	3.05E+01	0.00E+00
0.004	73	83	0.00E+00	1001	2.31E+01	0.00E+00
0.004	72	74	0.00E+00	1001	2.62E+01	0.00E+00
0.004	28	83	0.00E+00	1001	2.97E+01	0.00E+00
0.004	32	84	0.00E+00	1001	2.75E+01	0.00E+00
0.004	12	85	0.00E+00	1001	3.28E+01	0.00E+00
0.004	52	83	0.00E+00	1001	3.09E+01	0.00E+00
0.004	44	76	0.00E+00	1001	2.87E+01	0.00E+00
0.004	19	83	0.00E+00	1001	3.04E+01	0.00E+00
0.004	30	82	0.00E+00	1001	3.07E+01	0.00E+00
0.004	63	80	0.00E+00	1001	2.66E+01	0.00E+00
0.004	70	79	0.00E+00	1001	2.51E+01	0.00E+00
0.004	40	82	0.00E+00	1001	2.84E+01	0.00E+00
0.004	55	78	0.00E+00	1001	2.61E+01	0.00E+00
0.006	28	80	0.00E+00	1001	2.28E+01	0.00E+00
0.006	53	77	0.00E+00	1001	2.02E+01	0.00E+00
0.006	65	81	0.00E+00	1001	1.78E+01	0.00E+00
0.006	57	81	0.00E+00	1001	2.03E+01	0.00E+00
0.006	42	83	0.00E+00	1001	1.96E+01	0.00E+00
0.006	56	76	0.00E+00	1001	2.05E+01	0.00E+00
0.006	79	81	0.00E+00	1001	1.86E+01	0.00E+00
0.006	66	75	0.00E+00	1001	2.07E+01	0.00E+00
0.006	45	81	0.00E+00	1001	2.11E+01	0.00E+00
0.006	76	82	0.00E+00	1001	1.84E+01	0.00E+00
0.006	78	79	0.00E+00	1001	1.94E+01	0.00E+00
0.006	54	82	0.00E+00	1001	2.27E+01	0.00E+00
0.006	56	79	0.00E+00	1001	2.09E+01	0.00E+00
0.006	49	84	0.00E+00	1001	2.06E+01	0.00E+00
0.006	53	82	0.00E+00	1001	2.06E+01	0.00E+00
0.006	50	80	0.00E+00	1001	1.97E+01	0.00E+00
0.006	32	82	0.00E+00	1001	2.21E+01	0.00E+00
0.006	23	80	0.00E+00	1001	2.37E+01	0.00E+00
0.006	71	80	0.00E+00	1001	2.07E+01	0.00E+00
0.006	36	78	0.00E+00	1001	2.13E+01	0.00E+00
0.008	46	86	0.00E+00	1001	1.61E+01	0.00E+00
0.008	49	83	0.00E+00	1001	1.77E+01	0.00E+00
0.008	69	80	0.00E+00	1001	1.48E+01	0.00E+00
0.008	44	77	0.00E+00	1001	1.67E+01	0.00E+00
0.008	55	84	0.00E+00	1001	1.83E+01	0.00E+00
0.008	49	80	0.00E+00	1001	1.70E+01	0.00E+00
0.008	59	77	0.00E+00	1001	1.84E+01	0.00E+00
0.008	85	86	0.00E+00	1001	1.63E+01	0.00E+00
0.008	51	80	0.00E+00	1001	1.80E+01	0.00E+00
0.008	43	79	0.00E+00	1001	1.90E+01	0.00E+00
0.008	47	82	0.00E+00	1001	1.72E+01	0.00E+00
0.008	77	79	0.00E+00	1001	1.59E+01	0.00E+00
0.008	50	79	0.00E+00	1001	1.77E+01	0.00E+00
0.008	45	81	0.00E+00	1001	1.81E+01	0.00E+00
0.008	44	84	0.00E+00	1001	1.82E+01	0.00E+00

0.008	71	79	0.00E+00	1001	1.70E+01	0.00E+00
0.008	80	82	0.00E+00	1001	1.52E+01	0.00E+00
0.008	76	79	0.00E+00	1001	1.72E+01	0.00E+00
0.008	76	82	0.00E+00	1001	1.50E+01	0.00E+00
0.008	79	83	0.00E+00	1001	1.55E+01	0.00E+00
0.010	55	80	0.00E+00	1001	1.57E+01	0.00E+00
0.010	57	80	0.00E+00	1001	1.38E+01	0.00E+00
0.010	81	83	0.00E+00	1001	1.43E+01	0.00E+00
0.010	54	81	0.00E+00	1001	1.43E+01	0.00E+00
0.010	60	85	0.00E+00	1001	1.38E+01	0.00E+00
0.010	54	82	0.00E+00	1001	1.46E+01	0.00E+00
0.010	52	76	0.00E+00	1001	1.52E+01	0.00E+00
0.010	37	81	0.00E+00	1001	1.59E+01	0.00E+00
0.010	54	79	0.00E+00	1001	1.43E+01	0.00E+00
0.010	70	83	0.00E+00	1001	1.41E+01	0.00E+00
0.010	31	82	0.00E+00	1001	1.59E+01	0.00E+00
0.010	55	87	0.00E+00	1001	1.47E+01	0.00E+00
0.010	36	76	0.00E+00	1001	1.63E+01	0.00E+00
0.010	78	81	0.00E+00	1001	1.47E+01	0.00E+00
0.010	86	87	0.00E+00	1001	1.43E+01	0.00E+00
0.010	45	79	0.00E+00	1001	1.69E+01	0.00E+00
0.010	42	80	0.00E+00	1001	1.52E+01	0.00E+00
0.010	82	84	0.00E+00	1001	1.39E+01	0.00E+00
0.010	55	82	0.00E+00	1001	1.59E+01	0.00E+00
0.010	43	83	0.00E+00	1001	1.47E+01	0.00E+00
0.012	53	78	0.00E+00	1001	1.28E+01	0.00E+00
0.012	49	83	0.00E+00	1001	1.33E+01	0.00E+00
0.012	51	79	0.00E+00	1001	1.41E+01	0.00E+00
0.012	76	80	0.00E+00	1001	1.41E+01	0.00E+00
0.012	70	82	0.00E+00	1001	1.18E+01	0.00E+00
0.012	78	84	0.00E+00	1001	1.29E+01	0.00E+00
0.012	43	79	0.00E+00	1001	1.42E+01	0.00E+00
0.012	39	84	0.00E+00	1001	1.33E+01	0.00E+00
0.012	54	80	0.00E+00	1001	1.27E+01	0.00E+00
0.012	81	86	0.00E+00	1001	1.26E+01	0.00E+00
0.012	56	78	0.00E+00	1001	1.37E+01	0.00E+00
0.012	71	80	0.00E+00	1001	1.33E+01	0.00E+00
0.012	77	82	0.00E+00	1001	1.28E+01	0.00E+00
0.012	87	86	0.00E+00	1001	1.31E+01	0.00E+00
0.012	77	82	0.00E+00	1001	1.41E+01	0.00E+00
0.012	77	83	0.00E+00	1001	1.27E+01	0.00E+00
0.012	72	80	0.00E+00	1001	1.38E+01	0.00E+00
0.012	70	79	0.00E+00	1001	1.34E+01	0.00E+00
0.012	86	87	0.00E+00	1001	1.32E+01	0.00E+00
0.012	44	80	0.00E+00	1001	1.26E+01	0.00E+00
0.014	51	82	0.00E+00	1001	1.23E+01	0.00E+00
0.014	77	82	0.00E+00	1001	1.15E+01	0.00E+00
0.014	76	81	0.00E+00	1001	1.13E+01	0.00E+00
0.014	71	81	0.00E+00	1001	1.21E+01	0.00E+00
0.014	67	79	0.00E+00	1001	1.24E+01	0.00E+00
0.014	49	83	0.00E+00	1001	1.26E+01	0.00E+00
0.014	78	80	0.00E+00	1001	1.16E+01	0.00E+00
0.014	75	84	0.00E+00	1001	1.16E+01	0.00E+00
0.014	67	80	0.00E+00	1001	1.24E+01	0.00E+00
0.014	56	85	0.00E+00	1001	1.19E+01	0.00E+00
0.014	69	83	0.00E+00	1001	1.23E+01	0.00E+00
0.014	67	79	0.00E+00	1001	1.23E+01	0.00E+00
0.014	47	86	0.00E+00	1001	1.17E+01	0.00E+00

0.014	73	80	0.00E+00	1001	1.21E+01	0.00E+00
0.014	85	86	0.00E+00	1001	1.20E+01	0.00E+00
0.014	81	83	0.00E+00	1001	1.23E+01	0.00E+00
0.014	66	83	0.00E+00	1001	1.32E+01	0.00E+00
0.014	77	81	0.00E+00	1001	1.09E+01	0.00E+00
0.014	43	81	0.00E+00	1001	1.27E+01	0.00E+00
0.014	33	82	0.00E+00	1001	1.30E+01	0.00E+00
0.016	65	81	0.00E+00	1001	1.08E+01	0.00E+00
0.016	65	81	0.00E+00	1001	1.15E+01	0.00E+00
0.016	73	81	0.00E+00	1001	1.11E+01	0.00E+00
0.016	81	83	0.00E+00	1001	1.06E+01	0.00E+00
0.016	48	78	0.00E+00	1001	1.16E+01	0.00E+00
0.016	51	80	0.00E+00	1001	1.11E+01	0.00E+00
0.016	47	80	0.00E+00	1001	1.20E+01	0.00E+00
0.016	72	84	0.00E+00	1001	1.04E+01	0.00E+00
0.016	64	82	0.00E+00	1001	1.16E+01	0.00E+00
0.016	65	76	0.00E+00	1001	1.13E+01	0.00E+00
0.016	42	84	0.00E+00	1001	1.23E+01	0.00E+00
0.016	78	83	0.00E+00	1001	1.14E+01	0.00E+00
0.016	75	83	0.00E+00	1001	1.02E+01	0.00E+00
0.016	55	81	0.00E+00	1001	1.15E+01	0.00E+00
0.016	87	87	0.00E+00	1001	1.00E+01	0.00E+00
0.016	64	85	0.00E+00	1001	1.03E+01	0.00E+00
0.016	81	83	0.00E+00	1001	1.02E+01	0.00E+00
0.016	56	78	0.00E+00	1001	1.18E+01	0.00E+00
0.016	40	84	0.00E+00	1001	1.12E+01	0.00E+00
0.016	65	82	0.00E+00	1001	1.15E+01	0.00E+00
0.018	74	79	0.00E+00	1001	1.09E+01	0.00E+00
0.018	78	81	0.00E+00	1001	1.01E+01	0.00E+00
0.018	51	81	0.00E+00	1001	1.03E+01	0.00E+00
0.018	77	80	0.00E+00	1001	1.02E+01	0.00E+00
0.018	77	84	0.00E+00	1001	9.71E+00	0.00E+00
0.018	46	81	0.00E+00	1001	1.08E+01	0.00E+00
0.018	84	85	0.00E+00	1001	9.99E+00	0.00E+00
0.018	47	80	0.00E+00	1001	1.12E+01	0.00E+00
0.018	57	81	0.00E+00	1001	1.06E+01	0.00E+00
0.018	81	84	0.00E+00	1001	1.07E+01	0.00E+00
0.018	58	79	0.00E+00	1001	1.07E+01	0.00E+00
0.018	47	82	0.00E+00	1001	1.01E+01	0.00E+00
0.018	54	82	0.00E+00	1001	1.12E+01	0.00E+00
0.018	80	84	0.00E+00	1001	1.01E+01	0.00E+00
0.018	84	85	0.00E+00	1001	9.48E+00	0.00E+00
0.018	57	82	0.00E+00	1001	1.11E+01	0.00E+00
0.018	86	86	0.00E+00	1001	8.91E+00	0.00E+00
0.018	82	86	0.00E+00	1001	1.00E+01	0.00E+00
0.018	74	84	0.00E+00	1001	1.06E+01	0.00E+00
0.018	80	83	0.00E+00	1001	1.03E+01	0.00E+00
0.020	45	88	0.00E+00	1001	8.85E+00	0.00E+00
0.020	62	79	0.00E+00	1001	9.80E+00	0.00E+00
0.020	55	82	0.00E+00	1001	1.04E+01	0.00E+00
0.020	58	83	0.00E+00	1001	1.01E+01	0.00E+00
0.020	64	79	0.00E+00	1001	1.03E+01	0.00E+00
0.020	48	80	0.00E+00	1001	1.05E+01	0.00E+00
0.020	70	83	0.00E+00	1001	1.02E+01	0.00E+00
0.020	73	83	0.00E+00	1001	9.40E+00	0.00E+00
0.020	53	82	0.00E+00	1001	1.02E+01	0.00E+00
0.020	77	81	0.00E+00	1001	1.04E+01	0.00E+00
0.020	77	82	0.00E+00	1001	9.90E+00	0.00E+00

0.020	81	85	0.00E+00	1001	9.86E+00	0.00E+00
0.020	60	77	0.00E+00	1001	1.01E+01	0.00E+00
0.020	76	80	0.00E+00	1001	9.66E+00	0.00E+00
0.020	74	80	0.00E+00	1001	9.81E+00	0.00E+00
0.020	77	82	0.00E+00	1001	1.01E+01	0.00E+00
0.020	62	80	0.00E+00	1001	9.89E+00	0.00E+00
0.020	62	81	0.00E+00	1001	9.50E+00	0.00E+00
0.020	58	76	0.00E+00	1001	1.11E+01	0.00E+00
0.020	77	79	0.00E+00	1001	1.08E+01	0.00E+00

Experiment 5.5.5

Movement probability	Average cooperation	Average relatedness	Average interaction length	Model time	Average cell population	Average number of partners
0.0	50	75	0.00E+00	1001	4.06E+01	0.00E+00
0.0	34	78	0.00E+00	1001	4.93E+01	0.00E+00
0.0	45	75	0.00E+00	1001	4.72E+01	0.00E+00
0.0	55	77	0.00E+00	1001	3.59E+01	0.00E+00
0.0	43	80	0.00E+00	1001	3.83E+01	0.00E+00
0.0	59	74	0.00E+00	1001	4.59E+01	0.00E+00
0.0	25	82	0.00E+00	1001	4.82E+01	0.00E+00
0.0	74	80	0.00E+00	1001	4.43E+01	0.00E+00
0.0	62	78	0.00E+00	1001	4.08E+01	0.00E+00
0.0	38	79	0.00E+00	1001	4.74E+01	0.00E+00
0.0	38	77	0.00E+00	1001	4.36E+01	0.00E+00
0.0	41	80	0.00E+00	1001	3.72E+01	0.00E+00
0.0	43	77	0.00E+00	1001	6.71E+01	0.00E+00
0.0	52	82	0.00E+00	1001	3.24E+01	0.00E+00
0.0	52	74	0.00E+00	1001	3.89E+01	0.00E+00
0.0	52	77	0.00E+00	1001	4.86E+01	0.00E+00
0.0	58	75	0.00E+00	1001	4.98E+01	0.00E+00
0.0	63	75	0.00E+00	1001	5.00E+01	0.00E+00
0.0	36	77	0.00E+00	1001	4.98E+01	0.00E+00
0.0	36	76	0.00E+00	1001	3.98E+01	0.00E+00
0.1	36	74	0.00E+00	1001	3.48E+00	0.00E+00
0.1	52	68	0.00E+00	1001	3.48E+00	0.00E+00
0.1	41	78	0.00E+00	1001	3.66E+00	0.00E+00
0.1	39	72	0.00E+00	1001	3.76E+00	0.00E+00
0.1	40	69	0.00E+00	1001	3.78E+00	0.00E+00
0.1	41	76	0.00E+00	1001	3.71E+00	0.00E+00
0.1	34	72	0.00E+00	1001	3.84E+00	0.00E+00
0.1	42	74	0.00E+00	1001	3.65E+00	0.00E+00
0.1	33	72	0.00E+00	1001	3.55E+00	0.00E+00
0.1	35	69	0.00E+00	1001	3.87E+00	0.00E+00
0.1	26	77	0.00E+00	1001	3.72E+00	0.00E+00
0.1	24	77	0.00E+00	1001	3.65E+00	0.00E+00
0.1	36	75	0.00E+00	1001	3.64E+00	0.00E+00
0.1	38	69	0.00E+00	1001	3.56E+00	0.00E+00
0.1	47	76	0.00E+00	1001	3.66E+00	0.00E+00
0.1	34	71	0.00E+00	1001	3.66E+00	0.00E+00
0.1	40	70	0.00E+00	1001	3.66E+00	0.00E+00
0.1	32	73	0.00E+00	1001	3.76E+00	0.00E+00
0.1	46	70	0.00E+00	1001	3.58E+00	0.00E+00
0.1	47	74	0.00E+00	1001	3.64E+00	0.00E+00
0.2	25	76	0.00E+00	1001	2.84E+00	0.00E+00
0.2	19	76	0.00E+00	1001	2.85E+00	0.00E+00
0.2	29	70	0.00E+00	1001	2.89E+00	0.00E+00
0.2	24	73	0.00E+00	1001	2.83E+00	0.00E+00
0.2	18	78	0.00E+00	1001	2.87E+00	0.00E+00

0.2	32	72	0.00E+00	1001	2.72E+00	0.00E+00
0.2	26	75	0.00E+00	1001	2.83E+00	0.00E+00
0.2	17	78	0.00E+00	1001	2.86E+00	0.00E+00
0.2	24	72	0.00E+00	1001	2.82E+00	0.00E+00
0.2	28	71	0.00E+00	1001	2.81E+00	0.00E+00
0.2	29	73	0.00E+00	1001	2.75E+00	0.00E+00
0.2	17	77	0.00E+00	1001	2.84E+00	0.00E+00
0.2	20	75	0.00E+00	1001	2.80E+00	0.00E+00
0.2	19	75	0.00E+00	1001	2.86E+00	0.00E+00
0.2	26	70	0.00E+00	1001	2.79E+00	0.00E+00
0.2	36	73	0.00E+00	1001	2.76E+00	0.00E+00
0.2	30	74	0.00E+00	1001	2.79E+00	0.00E+00
0.2	18	76	0.00E+00	1001	2.82E+00	0.00E+00
0.2	18	76	0.00E+00	1001	2.92E+00	0.00E+00
0.2	32	70	0.00E+00	1001	2.78E+00	0.00E+00
0.3	15	78	0.00E+00	1001	2.42E+00	0.00E+00
0.3	17	77	0.00E+00	1001	2.48E+00	0.00E+00
0.3	19	75	0.00E+00	1001	2.53E+00	0.00E+00
0.3	19	76	0.00E+00	1001	2.48E+00	0.00E+00
0.3	20	76	0.00E+00	1001	2.45E+00	0.00E+00
0.3	20	72	0.00E+00	1001	2.42E+00	0.00E+00
0.3	18	77	0.00E+00	1001	2.44E+00	0.00E+00
0.3	20	74	0.00E+00	1001	2.41E+00	0.00E+00
0.3	14	80	0.00E+00	1001	2.42E+00	0.00E+00
0.3	22	73	0.00E+00	1001	2.44E+00	0.00E+00
0.3	16	76	0.00E+00	1001	2.45E+00	0.00E+00
0.3	13	80	0.00E+00	1001	2.44E+00	0.00E+00
0.3	16	78	0.00E+00	1001	2.46E+00	0.00E+00
0.3	21	72	0.00E+00	1001	2.44E+00	0.00E+00
0.3	17	75	0.00E+00	1001	2.41E+00	0.00E+00
0.3	22	72	0.00E+00	1001	2.45E+00	0.00E+00
0.3	17	77	0.00E+00	1001	2.44E+00	0.00E+00
0.3	20	74	0.00E+00	1001	2.52E+00	0.00E+00
0.3	17	77	0.00E+00	1001	2.44E+00	0.00E+00
0.3	16	77	0.00E+00	1001	2.51E+00	0.00E+00
0.4	14	79	0.00E+00	1001	2.26E+00	0.00E+00
0.4	13	79	0.00E+00	1001	2.24E+00	0.00E+00
0.4	14	78	0.00E+00	1001	2.26E+00	0.00E+00
0.4	13	79	0.00E+00	1001	2.28E+00	0.00E+00
0.4	11	82	0.00E+00	1001	2.29E+00	0.00E+00
0.4	19	76	0.00E+00	1001	2.25E+00	0.00E+00
0.4	8	86	0.00E+00	1001	2.25E+00	0.00E+00
0.4	11	82	0.00E+00	1001	2.29E+00	0.00E+00
0.4	15	77	0.00E+00	1001	2.28E+00	0.00E+00
0.4	15	77	0.00E+00	1001	2.25E+00	0.00E+00
0.4	16	76	0.00E+00	1001	2.27E+00	0.00E+00
0.4	13	80	0.00E+00	1001	2.26E+00	0.00E+00
0.4	17	77	0.00E+00	1001	2.23E+00	0.00E+00
0.4	10	83	0.00E+00	1001	2.30E+00	0.00E+00
0.4	18	75	0.00E+00	1001	2.29E+00	0.00E+00
0.4	10	83	0.00E+00	1001	2.26E+00	0.00E+00
0.4	13	80	0.00E+00	1001	2.25E+00	0.00E+00
0.4	15	76	0.00E+00	1001	2.28E+00	0.00E+00
0.4	12	80	0.00E+00	1001	2.28E+00	0.00E+00
0.4	19	74	0.00E+00	1001	2.28E+00	0.00E+00
0.5	10	82	0.00E+00	1001	2.20E+00	0.00E+00
0.5	14	78	0.00E+00	1001	2.18E+00	0.00E+00
0.5	13	80	0.00E+00	1001	2.17E+00	0.00E+00

0.5	12	81	0.00E+00	1001	2.15E+00	0.00E+00
0.5	14	78	0.00E+00	1001	2.16E+00	0.00E+00
0.5	15	78	0.00E+00	1001	2.17E+00	0.00E+00
0.5	7	86	0.00E+00	1001	2.17E+00	0.00E+00
0.5	13	80	0.00E+00	1001	2.17E+00	0.00E+00
0.5	9	83	0.00E+00	1001	2.18E+00	0.00E+00
0.5	12	80	0.00E+00	1001	2.19E+00	0.00E+00
0.5	11	81	0.00E+00	1001	2.16E+00	0.00E+00
0.5	17	75	0.00E+00	1001	2.19E+00	0.00E+00
0.5	12	79	0.00E+00	1001	2.17E+00	0.00E+00
0.5	11	81	0.00E+00	1001	2.17E+00	0.00E+00
0.5	11	82	0.00E+00	1001	2.16E+00	0.00E+00
0.5	9	84	0.00E+00	1001	2.16E+00	0.00E+00
0.5	15	77	0.00E+00	1001	2.16E+00	0.00E+00
0.5	13	79	0.00E+00	1001	2.16E+00	0.00E+00
0.5	11	81	0.00E+00	1001	2.15E+00	0.00E+00
0.5	9	84	0.00E+00	1001	2.18E+00	0.00E+00
0.6	9	84	0.00E+00	1001	2.11E+00	0.00E+00
0.6	9	84	0.00E+00	1001	2.12E+00	0.00E+00
0.6	11	81	0.00E+00	1001	2.11E+00	0.00E+00
0.6	10	82	0.00E+00	1001	2.13E+00	0.00E+00
0.6	11	81	0.00E+00	1001	2.11E+00	0.00E+00
0.6	10	81	0.00E+00	1001	2.13E+00	0.00E+00
0.6	11	80	0.00E+00	1001	2.12E+00	0.00E+00
0.6	11	81	0.00E+00	1001	2.12E+00	0.00E+00
0.6	12	80	0.00E+00	1001	2.11E+00	0.00E+00
0.6	15	78	0.00E+00	1001	2.11E+00	0.00E+00
0.6	12	79	0.00E+00	1001	2.11E+00	0.00E+00
0.6	10	83	0.00E+00	1001	2.10E+00	0.00E+00
0.6	12	80	0.00E+00	1001	2.12E+00	0.00E+00
0.6	10	82	0.00E+00	1001	2.13E+00	0.00E+00
0.6	11	81	0.00E+00	1001	2.12E+00	0.00E+00
0.6	14	78	0.00E+00	1001	2.13E+00	0.00E+00
0.6	13	80	0.00E+00	1001	2.13E+00	0.00E+00
0.6	10	83	0.00E+00	1001	2.13E+00	0.00E+00
0.6	11	81	0.00E+00	1001	2.12E+00	0.00E+00
0.6	9	83	0.00E+00	1001	2.12E+00	0.00E+00
0.7	14	76	0.00E+00	1001	2.09E+00	0.00E+00
0.7	9	83	0.00E+00	1001	2.10E+00	0.00E+00
0.7	10	82	0.00E+00	1001	2.08E+00	0.00E+00
0.7	16	76	0.00E+00	1001	2.10E+00	0.00E+00
0.7	8	85	0.00E+00	1001	2.09E+00	0.00E+00
0.7	9	83	0.00E+00	1001	2.09E+00	0.00E+00
0.7	10	82	0.00E+00	1001	2.10E+00	0.00E+00
0.7	10	81	0.00E+00	1001	2.10E+00	0.00E+00
0.7	10	82	0.00E+00	1001	2.08E+00	0.00E+00
0.7	12	81	0.00E+00	1001	2.09E+00	0.00E+00
0.7	11	82	0.00E+00	1001	2.09E+00	0.00E+00
0.7	11	82	0.00E+00	1001	2.09E+00	0.00E+00
0.7	8	85	0.00E+00	1001	2.09E+00	0.00E+00
0.7	8	84	0.00E+00	1001	2.08E+00	0.00E+00
0.7	11	81	0.00E+00	1001	2.09E+00	0.00E+00
0.7	11	81	0.00E+00	1001	2.09E+00	0.00E+00
0.7	10	82	0.00E+00	1001	2.08E+00	0.00E+00
0.7	9	84	0.00E+00	1001	2.09E+00	0.00E+00
0.7	12	79	0.00E+00	1001	2.10E+00	0.00E+00
0.7	13	80	0.00E+00	1001	2.09E+00	0.00E+00
0.8	11	79	0.00E+00	1001	2.08E+00	0.00E+00

0.8	10	83	0.00E+00	1001	2.07E+00	0.00E+00
0.8	10	82	0.00E+00	1001	2.08E+00	0.00E+00
0.8	10	82	0.00E+00	1001	2.08E+00	0.00E+00
0.8	12	81	0.00E+00	1001	2.08E+00	0.00E+00
0.8	10	82	0.00E+00	1001	2.08E+00	0.00E+00
0.8	9	83	0.00E+00	1001	2.07E+00	0.00E+00
0.8	8	84	0.00E+00	1001	2.07E+00	0.00E+00
0.8	9	84	0.00E+00	1001	2.07E+00	0.00E+00
0.8	10	82	0.00E+00	1001	2.07E+00	0.00E+00
0.8	9	84	0.00E+00	1001	2.07E+00	0.00E+00
0.8	8	85	0.00E+00	1001	2.07E+00	0.00E+00
0.8	12	79	0.00E+00	1001	2.08E+00	0.00E+00
0.8	10	82	0.00E+00	1001	2.07E+00	0.00E+00
0.8	8	85	0.00E+00	1001	2.07E+00	0.00E+00
0.8	9	85	0.00E+00	1001	2.07E+00	0.00E+00
0.8	11	80	0.00E+00	1001	2.07E+00	0.00E+00
0.8	10	81	0.00E+00	1001	2.07E+00	0.00E+00
0.8	13	79	0.00E+00	1001	2.07E+00	0.00E+00
0.8	10	82	0.00E+00	1001	2.07E+00	0.00E+00
0.9	9	84	0.00E+00	1001	2.07E+00	0.00E+00
0.9	9	84	0.00E+00	1001	2.06E+00	0.00E+00
0.9	9	84	0.00E+00	1001	2.07E+00	0.00E+00
0.9	6	87	0.00E+00	1001	2.06E+00	0.00E+00
0.9	9	85	0.00E+00	1001	2.06E+00	0.00E+00
0.9	6	87	0.00E+00	1001	2.06E+00	0.00E+00
0.9	9	83	0.00E+00	1001	2.05E+00	0.00E+00
0.9	8	85	0.00E+00	1001	2.07E+00	0.00E+00
0.9	8	85	0.00E+00	1001	2.06E+00	0.00E+00
0.9	10	82	0.00E+00	1001	2.07E+00	0.00E+00
0.9	11	81	0.00E+00	1001	2.07E+00	0.00E+00
0.9	11	82	0.00E+00	1001	2.07E+00	0.00E+00
0.9	8	85	0.00E+00	1001	2.06E+00	0.00E+00
0.9	9	82	0.00E+00	1001	2.06E+00	0.00E+00
0.9	10	83	0.00E+00	1001	2.06E+00	0.00E+00
0.9	9	83	0.00E+00	1001	2.07E+00	0.00E+00
0.9	13	79	0.00E+00	1001	2.07E+00	0.00E+00
0.9	10	83	0.00E+00	1001	2.07E+00	0.00E+00
0.9	13	78	0.00E+00	1001	2.06E+00	0.00E+00
0.9	6	87	0.00E+00	1001	2.05E+00	0.00E+00
1.0	9	83	0.00E+00	1001	2.06E+00	0.00E+00
1.0	9	83	0.00E+00	1001	2.06E+00	0.00E+00
1.0	7	86	0.00E+00	1001	2.05E+00	0.00E+00
1.0	9	83	0.00E+00	1001	2.06E+00	0.00E+00
1.0	12	81	0.00E+00	1001	2.06E+00	0.00E+00
1.0	9	84	0.00E+00	1001	2.06E+00	0.00E+00
1.0	9	84	0.00E+00	1001	2.06E+00	0.00E+00
1.0	8	85	0.00E+00	1001	2.05E+00	0.00E+00
1.0	6	87	0.00E+00	1001	2.06E+00	0.00E+00
1.0	8	85	0.00E+00	1001	2.07E+00	0.00E+00
1.0	8	84	0.00E+00	1001	2.06E+00	0.00E+00
1.0	7	85	0.00E+00	1001	2.05E+00	0.00E+00
1.0	8	85	0.00E+00	1001	2.06E+00	0.00E+00
1.0	6	88	0.00E+00	1001	2.06E+00	0.00E+00
1.0	7	86	0.00E+00	1001	2.05E+00	0.00E+00
1.0	7	86	0.00E+00	1001	2.05E+00	0.00E+00
1.0	7	86	0.00E+00	1001	2.05E+00	0.00E+00
1.0	8	86	0.00E+00	1001	2.05E+00	0.00E+00
1.0	8	85	0.00E+00	1001	2.05E+00	0.00E+00

1.0	7	86	0.00E+00	1001	2.05E+00	0.00E+00

Experiment 5.6.2

Movement probability	Average cooperation	Average relatedness	Average interaction length	Model time	Average cell population	Average number of partners
0.0	29	64	2.61E+00	1001	2.06E+00	9.47E-01
0.0	19	65	2.42E+00	1001	2.02E+00	9.38E-01
0.0	35	63	2.73E+00	1001	2.13E+00	9.69E-01
0.0	29	66	2.62E+00	1001	2.07E+00	9.53E-01
0.0	26	64	2.54E+00	1001	2.06E+00	9.55E-01
0.0	20	67	2.45E+00	1001	2.03E+00	9.34E-01
0.0	31	62	2.63E+00	1001	2.08E+00	9.54E-01
0.0	20	64	2.44E+00	1001	2.03E+00	9.34E-01
0.0	26	63	2.56E+00	1001	2.07E+00	9.48E-01
0.0	36	64	2.72E+00	1001	2.11E+00	9.67E-01
0.0	19	67	2.41E+00	1001	2.04E+00	9.36E-01
0.0	26	65	2.54E+00	1001	2.05E+00	9.46E-01
0.0	25	61	2.54E+00	1001	2.05E+00	9.46E-01
0.0	29	64	2.62E+00	1001	2.07E+00	9.46E-01
0.0	25	64	2.53E+00	1001	2.05E+00	9.44E-01
0.0	35	61	2.76E+00	1001	2.11E+00	9.66E-01
0.0	28	63	2.58E+00	1001	2.05E+00	9.45E-01
0.0	35	67	2.73E+00	1001	2.09E+00	9.51E-01
0.0	20	65	2.43E+00	1001	2.04E+00	9.40E-01
0.0	28	65	2.60E+00	1001	2.07E+00	9.45E-01
0.1	19	62	1.92E+00	1001	2.00E+00	1.16E+00
0.1	17	65	1.91E+00	1001	1.98E+00	1.14E+00
0.1	23	62	1.98E+00	1001	2.00E+00	1.18E+00
0.1	22	62	1.96E+00	1001	2.01E+00	1.17E+00
0.1	23	64	1.96E+00	1001	2.00E+00	1.16E+00
0.1	20	64	1.95E+00	1001	1.99E+00	1.16E+00
0.1	19	65	1.95E+00	1001	2.00E+00	1.15E+00
0.1	18	64	1.92E+00	1001	1.99E+00	1.15E+00
0.1	21	63	1.96E+00	1001	2.00E+00	1.17E+00
0.1	19	68	1.93E+00	1001	1.98E+00	1.14E+00
0.1	21	63	1.94E+00	1001	1.99E+00	1.16E+00
0.1	14	70	1.90E+00	1001	1.97E+00	1.12E+00
0.1	22	65	1.96E+00	1001	2.00E+00	1.17E+00
0.1	20	64	1.94E+00	1001	2.00E+00	1.16E+00
0.1	17	66	1.91E+00	1001	1.97E+00	1.14E+00
0.1	18	66	1.92E+00	1001	1.98E+00	1.15E+00
0.1	18	64	1.94E+00	1001	1.98E+00	1.14E+00
0.1	18	67	1.92E+00	1001	1.99E+00	1.15E+00
0.1	19	65	1.93E+00	1001	1.98E+00	1.15E+00
0.1	27	66	2.01E+00	1001	2.02E+00	1.19E+00
0.2	14	67	1.60E+00	1001	1.96E+00	1.34E+00
0.2	15	65	1.60E+00	1001	1.95E+00	1.34E+00
0.2	18	65	1.62E+00	1001	1.97E+00	1.35E+00
0.2	23	65	1.65E+00	1001	1.98E+00	1.38E+00
0.2	15	66	1.60E+00	1001	1.96E+00	1.35E+00
0.2	14	69	1.60E+00	1001	1.96E+00	1.33E+00
0.2	24	64	1.64E+00	1001	1.99E+00	1.40E+00
0.2	17	66	1.61E+00	1001	1.97E+00	1.36E+00
0.2	14	65	1.60E+00	1001	1.96E+00	1.34E+00
0.2	16	63	1.62E+00	1001	1.96E+00	1.33E+00
0.2	15	64	1.60E+00	1001	1.96E+00	1.33E+00
0.2	19	65	1.62E+00	1001	1.96E+00	1.35E+00
0.2	16	65	1.61E+00	1001	1.96E+00	1.34E+00

0.2	18	64	1.62E+00	1001	1.97E+00	1.35E+00
0.2	22	65	1.65E+00	1001	1.98E+00	1.39E+00
0.2	15	68	1.59E+00	1001	1.96E+00	1.35E+00
0.2	15	67	1.60E+00	1001	1.96E+00	1.35E+00
0.2	12	69	1.58E+00	1001	1.96E+00	1.32E+00
0.2	16	68	1.61E+00	1001	1.97E+00	1.34E+00
0.2	21	63	1.63E+00	1001	1.97E+00	1.38E+00
0.3	15	66	1.42E+00	1001	1.95E+00	1.49E+00
0.3	15	66	1.42E+00	1001	1.95E+00	1.51E+00
0.3	13	68	1.41E+00	1001	1.94E+00	1.49E+00
0.3	16	66	1.42E+00	1001	1.95E+00	1.51E+00
0.3	13	68	1.40E+00	1001	1.94E+00	1.49E+00
0.3	19	64	1.42E+00	1001	1.96E+00	1.54E+00
0.3	24	63	1.44E+00	1001	1.97E+00	1.58E+00
0.3	16	67	1.42E+00	1001	1.96E+00	1.51E+00
0.3	13	68	1.41E+00	1001	1.95E+00	1.49E+00
0.3	13	68	1.41E+00	1001	1.95E+00	1.49E+00
0.3	18	65	1.42E+00	1001	1.95E+00	1.53E+00
0.3	15	65	1.42E+00	1001	1.95E+00	1.51E+00
0.3	16	66	1.41E+00	1001	1.95E+00	1.51E+00
0.3	16	62	1.42E+00	1001	1.95E+00	1.52E+00
0.3	15	65	1.42E+00	1001	1.95E+00	1.50E+00
0.3	15	65	1.42E+00	1001	1.96E+00	1.51E+00
0.3	14	66	1.41E+00	1001	1.95E+00	1.50E+00
0.3	14	67	1.41E+00	1001	1.94E+00	1.50E+00
0.3	20	62	1.43E+00	1001	1.96E+00	1.55E+00
0.3	15	65	1.42E+00	1001	1.95E+00	1.51E+00
0.4	11	68	1.28E+00	1001	1.94E+00	1.61E+00
0.4	13	65	1.29E+00	1001	1.94E+00	1.62E+00
0.4	12	67	1.28E+00	1001	1.93E+00	1.62E+00
0.4	16	64	1.29E+00	1001	1.94E+00	1.66E+00
0.4	9	69	1.28E+00	1001	1.92E+00	1.58E+00
0.4	11	68	1.28E+00	1001	1.94E+00	1.61E+00
0.4	10	68	1.28E+00	1001	1.92E+00	1.59E+00
0.4	16	63	1.29E+00	1001	1.95E+00	1.67E+00
0.4	12	65	1.29E+00	1001	1.94E+00	1.63E+00
0.4	11	67	1.28E+00	1001	1.93E+00	1.60E+00
0.4	16	66	1.29E+00	1001	1.95E+00	1.66E+00
0.4	14	66	1.29E+00	1001	1.94E+00	1.64E+00
0.4	13	65	1.29E+00	1001	1.93E+00	1.62E+00
0.4	13	64	1.29E+00	1001	1.94E+00	1.63E+00
0.4	11	67	1.28E+00	1001	1.93E+00	1.61E+00
0.4	13	64	1.29E+00	1001	1.93E+00	1.62E+00
0.4	11	66	1.29E+00	1001	1.93E+00	1.61E+00
0.4	15	62	1.29E+00	1001	1.94E+00	1.66E+00
0.4	15	67	1.29E+00	1001	1.94E+00	1.65E+00
0.4	11	65	1.29E+00	1001	1.93E+00	1.61E+00
0.5	12	64	1.20E+00	1001	1.93E+00	1.72E+00
0.5	12	65	1.20E+00	1001	1.94E+00	1.73E+00
0.5	11	66	1.20E+00	1001	1.93E+00	1.72E+00
0.5	11	68	1.20E+00	1001	1.93E+00	1.71E+00
0.5	11	64	1.20E+00	1001	1.92E+00	1.71E+00
0.5	11	67	1.20E+00	1001	1.93E+00	1.72E+00
0.5	12	64	1.20E+00	1001	1.93E+00	1.73E+00
0.5	11	67	1.20E+00	1001	1.93E+00	1.72E+00
0.5	9	69	1.20E+00	1001	1.92E+00	1.69E+00
0.5	11	68	1.20E+00	1001	1.93E+00	1.72E+00
0.5	11	65	1.20E+00	1001	1.93E+00	1.72E+00

0.5	10	67	1.20E+00	1001	1.93E+00	1.71E+00
0.5	11	64	1.20E+00	1001	1.92E+00	1.71E+00
0.5	11	64	1.20E+00	1001	1.94E+00	1.74E+00
0.5	12	65	1.20E+00	1001	1.93E+00	1.74E+00
0.5	11	71	1.20E+00	1001	1.93E+00	1.71E+00
0.5	15	66	1.20E+00	1001	1.94E+00	1.77E+00
0.5	11	65	1.20E+00	1001	1.93E+00	1.71E+00
0.5	11	65	1.20E+00	1001	1.93E+00	1.72E+00
0.5	11	64	1.20E+00	1001	1.93E+00	1.71E+00
0.6	11	66	1.14E+00	1001	1.93E+00	1.80E+00
0.6	11	68	1.14E+00	1001	1.93E+00	1.81E+00
0.6	10	67	1.14E+00	1001	1.92E+00	1.78E+00
0.6	9	68	1.14E+00	1001	1.92E+00	1.77E+00
0.6	9	66	1.14E+00	1001	1.92E+00	1.78E+00
0.6	11	66	1.14E+00	1001	1.93E+00	1.80E+00
0.6	9	67	1.14E+00	1001	1.92E+00	1.79E+00
0.6	10	67	1.14E+00	1001	1.92E+00	1.78E+00
0.6	10	66	1.14E+00	1001	1.93E+00	1.79E+00
0.6	9	66	1.14E+00	1001	1.92E+00	1.78E+00
0.6	10	67	1.14E+00	1001	1.92E+00	1.80E+00
0.6	9	65	1.14E+00	1001	1.92E+00	1.78E+00
0.6	9	64	1.14E+00	1001	1.92E+00	1.78E+00
0.6	11	67	1.14E+00	1001	1.92E+00	1.80E+00
0.6	10	63	1.14E+00	1001	1.92E+00	1.80E+00
0.6	10	67	1.14E+00	1001	1.92E+00	1.79E+00
0.6	10	64	1.14E+00	1001	1.92E+00	1.80E+00
0.6	9	65	1.14E+00	1001	1.92E+00	1.77E+00
0.6	8	67	1.14E+00	1001	1.92E+00	1.77E+00
0.6	9	64	1.14E+00	1001	1.92E+00	1.78E+00
0.7	10	63	1.10E+00	1001	1.91E+00	1.83E+00
0.7	9	66	1.10E+00	1001	1.92E+00	1.84E+00
0.7	10	64	1.10E+00	1001	1.92E+00	1.86E+00
0.7	10	63	1.10E+00	1001	1.92E+00	1.85E+00
0.7	10	65	1.10E+00	1001	1.92E+00	1.85E+00
0.7	7	69	1.10E+00	1001	1.92E+00	1.82E+00
0.7	9	68	1.10E+00	1001	1.92E+00	1.84E+00
0.7	9	66	1.10E+00	1001	1.92E+00	1.84E+00
0.7	8	66	1.10E+00	1001	1.92E+00	1.82E+00
0.7	9	66	1.10E+00	1001	1.92E+00	1.84E+00
0.7	12	67	1.10E+00	1001	1.93E+00	1.87E+00
0.7	10	63	1.10E+00	1001	1.92E+00	1.86E+00
0.7	9	67	1.10E+00	1001	1.92E+00	1.83E+00
0.7	8	64	1.10E+00	1001	1.92E+00	1.83E+00
0.7	8	66	1.10E+00	1001	1.92E+00	1.81E+00
0.7	9	64	1.10E+00	1001	1.91E+00	1.83E+00
0.7	7	63	1.10E+00	1001	1.92E+00	1.81E+00
0.7	7	67	1.10E+00	1001	1.92E+00	1.81E+00
0.7	8	66	1.10E+00	1001	1.91E+00	1.82E+00
0.7	9	64	1.10E+00	1001	1.92E+00	1.83E+00
0.8	8	67	1.08E+00	1001	1.92E+00	1.86E+00
0.8	6	67	1.08E+00	1001	1.91E+00	1.84E+00
0.8	9	65	1.08E+00	1001	1.92E+00	1.87E+00
0.8	9	65	1.08E+00	1001	1.93E+00	1.89E+00
0.8	7	66	1.08E+00	1001	1.91E+00	1.85E+00
0.8	7	64	1.08E+00	1001	1.92E+00	1.85E+00
0.8	8	64	1.08E+00	1001	1.92E+00	1.86E+00
0.8	9	63	1.08E+00	1001	1.92E+00	1.87E+00
0.8	9	65	1.08E+00	1001	1.92E+00	1.89E+00

0.8	9	64	1.08E+00	1001	1.91E+00	1.87E+00
0.8	9	64	1.08E+00	1001	1.92E+00	1.87E+00
0.8	8	66	1.08E+00	1001	1.91E+00	1.84E+00
0.8	10	66	1.08E+00	1001	1.92E+00	1.89E+00
0.8	7	67	1.08E+00	1001	1.91E+00	1.87E+00
0.8	9	65	1.08E+00	1001	1.92E+00	1.88E+00
0.8	7	65	1.08E+00	1001	1.91E+00	1.85E+00
0.8	9	64	1.08E+00	1001	1.92E+00	1.88E+00
0.8	8	64	1.08E+00	1001	1.92E+00	1.85E+00
0.8	6	66	1.08E+00	1001	1.91E+00	1.83E+00
0.8	6	68	1.08E+00	1001	1.91E+00	1.84E+00
0.9	10	63	1.07E+00	1001	1.92E+00	1.89E+00
0.9	7	66	1.07E+00	1001	1.92E+00	1.87E+00
0.9	9	66	1.07E+00	1001	1.92E+00	1.89E+00
0.9	10	67	1.07E+00	1001	1.92E+00	1.89E+00
0.9	10	70	1.07E+00	1001	1.92E+00	1.89E+00
0.9	7	65	1.07E+00	1001	1.91E+00	1.86E+00
0.9	9	65	1.07E+00	1001	1.92E+00	1.89E+00
0.9	8	67	1.07E+00	1001	1.92E+00	1.87E+00
0.9	9	61	1.07E+00	1001	1.92E+00	1.88E+00
0.9	8	66	1.07E+00	1001	1.91E+00	1.86E+00
0.9	10	66	1.07E+00	1001	1.91E+00	1.89E+00
0.9	9	63	1.07E+00	1001	1.92E+00	1.90E+00
0.9	8	66	1.07E+00	1001	1.91E+00	1.86E+00
0.9	8	65	1.07E+00	1001	1.91E+00	1.87E+00
0.9	8	69	1.07E+00	1001	1.92E+00	1.88E+00
0.9	7	66	1.07E+00	1001	1.91E+00	1.84E+00
0.9	8	63	1.07E+00	1001	1.91E+00	1.87E+00
0.9	6	67	1.07E+00	1001	1.92E+00	1.87E+00
0.9	6	66	1.07E+00	1001	1.91E+00	1.85E+00
0.9	8	66	1.07E+00	1001	1.92E+00	1.88E+00
1.0	8	66	1.08E+00	1001	1.91E+00	1.85E+00
1.0	8	66	1.08E+00	1001	1.91E+00	1.85E+00
1.0	8	65	1.08E+00	1001	1.92E+00	1.86E+00
1.0	8	67	1.08E+00	1001	1.92E+00	1.88E+00
1.0	8	65	1.08E+00	1001	1.92E+00	1.86E+00
1.0	9	67	1.08E+00	1001	1.92E+00	1.87E+00
1.0	8	68	1.08E+00	1001	1.92E+00	1.86E+00
1.0	8	65	1.08E+00	1001	1.91E+00	1.86E+00
1.0	7	67	1.08E+00	1001	1.91E+00	1.84E+00
1.0	9	66	1.08E+00	1001	1.92E+00	1.88E+00
1.0	8	67	1.08E+00	1001	1.92E+00	1.87E+00
1.0	9	68	1.08E+00	1001	1.91E+00	1.87E+00
1.0	10	65	1.08E+00	1001	1.92E+00	1.89E+00
1.0	8	63	1.08E+00	1001	1.92E+00	1.86E+00
1.0	9	67	1.08E+00	1001	1.92E+00	1.88E+00
1.0	6	65	1.08E+00	1001	1.91E+00	1.84E+00
1.0	8	65	1.08E+00	1001	1.92E+00	1.86E+00
1.0	10	67	1.08E+00	1001	1.92E+00	1.87E+00
1.0	8	62	1.08E+00	1001	1.92E+00	1.86E+00
1.0	10	65	1.08E+00	1001	1.92E+00	1.87E+00

Experiment 5.6.3

Movement probability	Average cooperation	Average relatedness	Average interaction length	Model time	Average cell population	Average number of partners
0.0	19	65	3.48E+00	1001	2.15E+00	1.10E+00
0.0	34	66	3.80E+00	1001	2.18E+00	1.09E+00
0.0	37	63	3.90E+00	1001	2.20E+00	1.11E+00

0.0	44	64	4.02E+00	1001	2.20E+00	1.10E+00
0.0	32	65	3.73E+00	1001	2.17E+00	1.09E+00
0.0	34	63	3.78E+00	1001	2.17E+00	1.10E+00
0.0	29	59	3.75E+00	1001	2.17E+00	1.10E+00
0.0	24	64	3.61E+00	1001	2.15E+00	1.10E+00
0.0	33	61	3.79E+00	1001	2.17E+00	1.09E+00
0.0	24	62	3.55E+00	1001	2.16E+00	1.11E+00
0.0	40	62	3.97E+00	1001	2.21E+00	1.11E+00
0.0	24	61	3.63E+00	1001	2.16E+00	1.09E+00
0.0	23	66	3.58E+00	1001	2.16E+00	1.10E+00
0.0	27	61	3.69E+00	1001	2.17E+00	1.11E+00
0.0	43	60	3.95E+00	1001	2.20E+00	1.09E+00
0.0	36	62	3.93E+00	1001	2.19E+00	1.10E+00
0.0	34	58	3.89E+00	1001	2.17E+00	1.08E+00
0.0	23	62	3.58E+00	1001	2.17E+00	1.12E+00
0.0	34	59	3.88E+00	1001	2.18E+00	1.09E+00
0.0	30	62	3.74E+00	1001	2.17E+00	1.10E+00
0.1	22	64	2.41E+00	1001	2.11E+00	1.63E+00
0.1	29	61	2.44E+00	1001	2.12E+00	1.66E+00
0.1	28	61	2.43E+00	1001	2.12E+00	1.68E+00
0.1	26	63	2.45E+00	1001	2.12E+00	1.63E+00
0.1	30	59	2.47E+00	1001	2.13E+00	1.66E+00
0.1	20	65	2.38E+00	1001	2.11E+00	1.61E+00
0.1	21	66	2.39E+00	1001	2.11E+00	1.61E+00
0.1	31	66	2.48E+00	1001	2.13E+00	1.67E+00
0.1	24	63	2.40E+00	1001	2.11E+00	1.64E+00
0.1	26	60	2.44E+00	1001	2.13E+00	1.63E+00
0.1	22	66	2.40E+00	1001	2.12E+00	1.62E+00
0.1	20	64	2.38E+00	1001	2.11E+00	1.61E+00
0.1	40	61	2.55E+00	1001	2.14E+00	1.71E+00
0.1	28	66	2.45E+00	1001	2.12E+00	1.63E+00
0.1	30	64	2.46E+00	1001	2.13E+00	1.68E+00
0.1	17	66	2.36E+00	1001	2.11E+00	1.60E+00
0.1	27	63	2.43E+00	1001	2.12E+00	1.63E+00
0.1	20	65	2.38E+00	1001	2.11E+00	1.62E+00
0.1	30	65	2.47E+00	1001	2.13E+00	1.66E+00
0.1	28	65	2.44E+00	1001	2.12E+00	1.64E+00
0.2	17	69	1.83E+00	1001	2.10E+00	2.06E+00
0.2	19	65	1.84E+00	1001	2.10E+00	2.07E+00
0.2	23	61	1.85E+00	1001	2.11E+00	2.11E+00
0.2	22	64	1.84E+00	1001	2.10E+00	2.13E+00
0.2	17	66	1.83E+00	1001	2.09E+00	2.07E+00
0.2	21	64	1.84E+00	1001	2.10E+00	2.10E+00
0.2	27	60	1.85E+00	1001	2.11E+00	2.15E+00
0.2	14	72	1.83E+00	1001	2.09E+00	2.02E+00
0.2	17	64	1.83E+00	1001	2.10E+00	2.07E+00
0.2	14	66	1.81E+00	1001	2.09E+00	2.05E+00
0.2	22	64	1.84E+00	1001	2.10E+00	2.09E+00
0.2	21	65	1.85E+00	1001	2.11E+00	2.11E+00
0.2	22	66	1.84E+00	1001	2.10E+00	2.13E+00
0.2	17	66	1.83E+00	1001	2.09E+00	2.07E+00
0.2	17	64	1.84E+00	1001	2.09E+00	2.05E+00
0.2	15	69	1.82E+00	1001	2.09E+00	2.03E+00
0.2	18	62	1.84E+00	1001	2.10E+00	2.06E+00
0.2	24	62	1.86E+00	1001	2.11E+00	2.13E+00
0.2	20	65	1.85E+00	1001	2.10E+00	2.08E+00
0.2	26	67	1.86E+00	1001	2.11E+00	2.13E+00
0.3	19	63	1.54E+00	1001	2.09E+00	2.47E+00

0.3	24	65	1.56E+00	1001	2.10E+00	2.53E+00
0.3	22	62	1.56E+00	1001	2.09E+00	2.49E+00
0.3	18	66	1.54E+00	1001	2.09E+00	2.46E+00
0.3	19	65	1.55E+00	1001	2.10E+00	2.47E+00
0.3	15	65	1.55E+00	1001	2.08E+00	2.43E+00
0.3	18	65	1.55E+00	1001	2.09E+00	2.44E+00
0.3	16	68	1.55E+00	1001	2.10E+00	2.44E+00
0.3	17	66	1.55E+00	1001	2.08E+00	2.44E+00
0.3	16	64	1.55E+00	1001	2.10E+00	2.43E+00
0.3	29	62	1.57E+00	1001	2.10E+00	2.59E+00
0.3	16	67	1.54E+00	1001	2.08E+00	2.42E+00
0.3	20	63	1.54E+00	1001	2.09E+00	2.47E+00
0.3	13	67	1.53E+00	1001	2.08E+00	2.41E+00
0.3	16	64	1.54E+00	1001	2.09E+00	2.45E+00
0.3	16	64	1.54E+00	1001	2.09E+00	2.44E+00
0.3	18	65	1.55E+00	1001	2.08E+00	2.45E+00
0.3	23	63	1.56E+00	1001	2.10E+00	2.50E+00
0.3	15	67	1.54E+00	1001	2.09E+00	2.43E+00
0.3	20	62	1.54E+00	1001	2.09E+00	2.48E+00
0.4	14	65	1.37E+00	1001	2.08E+00	2.72E+00
0.4	13	64	1.36E+00	1001	2.08E+00	2.68E+00
0.4	18	61	1.37E+00	1001	2.09E+00	2.77E+00
0.4	15	64	1.37E+00	1001	2.08E+00	2.71E+00
0.4	19	62	1.37E+00	1001	2.08E+00	2.76E+00
0.4	16	64	1.37E+00	1001	2.08E+00	2.72E+00
0.4	15	64	1.37E+00	1001	2.09E+00	2.74E+00
0.4	15	66	1.36E+00	1001	2.09E+00	2.74E+00
0.4	16	63	1.37E+00	1001	2.09E+00	2.73E+00
0.4	14	63	1.37E+00	1001	2.08E+00	2.72E+00
0.4	14	66	1.36E+00	1001	2.08E+00	2.70E+00
0.4	10	68	1.36E+00	1001	2.08E+00	2.65E+00
0.4	15	67	1.37E+00	1001	2.08E+00	2.74E+00
0.4	17	64	1.36E+00	1001	2.09E+00	2.75E+00
0.4	13	69	1.37E+00	1001	2.08E+00	2.71E+00
0.4	14	69	1.36E+00	1001	2.08E+00	2.70E+00
0.4	18	65	1.37E+00	1001	2.09E+00	2.79E+00
0.4	17	64	1.36E+00	1001	2.09E+00	2.78E+00
0.4	15	67	1.36E+00	1001	2.08E+00	2.72E+00
0.4	14	71	1.36E+00	1001	2.08E+00	2.71E+00
0.5	14	67	1.26E+00	1001	2.08E+00	2.94E+00
0.5	14	65	1.26E+00	1001	2.09E+00	2.94E+00
0.5	14	65	1.26E+00	1001	2.08E+00	2.95E+00
0.5	13	68	1.25E+00	1001	2.08E+00	2.94E+00
0.5	13	68	1.25E+00	1001	2.08E+00	2.93E+00
0.5	13	64	1.26E+00	1001	2.08E+00	2.97E+00
0.5	16	63	1.26E+00	1001	2.08E+00	2.96E+00
0.5	13	64	1.26E+00	1001	2.08E+00	2.91E+00
0.5	14	65	1.25E+00	1001	2.08E+00	2.96E+00
0.5	14	64	1.25E+00	1001	2.08E+00	2.97E+00
0.5	13	67	1.25E+00	1001	2.09E+00	2.94E+00
0.5	17	63	1.25E+00	1001	2.08E+00	3.01E+00
0.5	12	65	1.25E+00	1001	2.08E+00	2.94E+00
0.5	21	63	1.26E+00	1001	2.09E+00	3.06E+00
0.5	11	66	1.25E+00	1001	2.08E+00	2.90E+00
0.5	11	63	1.25E+00	1001	2.08E+00	2.93E+00
0.5	17	62	1.26E+00	1001	2.08E+00	2.99E+00
0.5	18	64	1.25E+00	1001	2.08E+00	3.03E+00
0.5	15	62	1.26E+00	1001	2.08E+00	2.96E+00

0.5	12	66	1.25E+00	1001	2.07E+00	2.90E+00
0.6	15	63	1.18E+00	1001	2.08E+00	3.12E+00
0.6	13	67	1.18E+00	1001	2.08E+00	3.09E+00
0.6	11	66	1.18E+00	1001	2.07E+00	3.09E+00
0.6	13	64	1.18E+00	1001	2.08E+00	3.12E+00
0.6	16	64	1.18E+00	1001	2.08E+00	3.19E+00
0.6	13	63	1.18E+00	1001	2.08E+00	3.12E+00
0.6	15	62	1.18E+00	1001	2.08E+00	3.18E+00
0.6	16	61	1.18E+00	1001	2.08E+00	3.18E+00
0.6	11	64	1.18E+00	1001	2.07E+00	3.09E+00
0.6	14	65	1.18E+00	1001	2.08E+00	3.13E+00
0.6	13	65	1.18E+00	1001	2.08E+00	3.13E+00
0.6	13	65	1.18E+00	1001	2.08E+00	3.09E+00
0.6	12	66	1.18E+00	1001	2.08E+00	3.10E+00
0.6	15	64	1.18E+00	1001	2.08E+00	3.14E+00
0.6	18	62	1.18E+00	1001	2.09E+00	3.19E+00
0.6	15	63	1.18E+00	1001	2.08E+00	3.16E+00
0.6	12	63	1.17E+00	1001	2.08E+00	3.12E+00
0.6	12	65	1.18E+00	1001	2.08E+00	3.11E+00
0.6	14	66	1.18E+00	1001	2.07E+00	3.12E+00
0.6	12	64	1.18E+00	1001	2.08E+00	3.10E+00
0.7	12	65	1.13E+00	1001	2.07E+00	3.24E+00
0.7	13	64	1.13E+00	1001	2.08E+00	3.29E+00
0.7	14	67	1.13E+00	1001	2.08E+00	3.26E+00
0.7	12	63	1.13E+00	1001	2.07E+00	3.23E+00
0.7	14	67	1.13E+00	1001	2.08E+00	3.24E+00
0.7	12	66	1.13E+00	1001	2.08E+00	3.22E+00
0.7	10	68	1.13E+00	1001	2.08E+00	3.21E+00
0.7	11	63	1.13E+00	1001	2.07E+00	3.20E+00
0.7	11	65	1.13E+00	1001	2.08E+00	3.21E+00
0.7	9	65	1.13E+00	1001	2.07E+00	3.16E+00
0.7	13	62	1.13E+00	1001	2.08E+00	3.22E+00
0.7	11	64	1.13E+00	1001	2.07E+00	3.22E+00
0.7	13	68	1.13E+00	1001	2.08E+00	3.23E+00
0.7	12	62	1.13E+00	1001	2.08E+00	3.24E+00
0.7	13	63	1.13E+00	1001	2.08E+00	3.26E+00
0.7	17	67	1.13E+00	1001	2.08E+00	3.33E+00
0.7	13	64	1.13E+00	1001	2.08E+00	3.27E+00
0.7	12	66	1.13E+00	1001	2.08E+00	3.23E+00
0.7	11	64	1.13E+00	1001	2.07E+00	3.22E+00
0.7	13	62	1.13E+00	1001	2.08E+00	3.23E+00
0.8	10	64	1.10E+00	1001	2.07E+00	3.28E+00
0.8	11	63	1.11E+00	1001	2.07E+00	3.29E+00
0.8	11	67	1.10E+00	1001	2.07E+00	3.26E+00
0.8	11	65	1.10E+00	1001	2.07E+00	3.29E+00
0.8	10	65	1.10E+00	1001	2.07E+00	3.28E+00
0.8	10	69	1.10E+00	1001	2.07E+00	3.27E+00
0.8	10	67	1.10E+00	1001	2.07E+00	3.25E+00
0.8	12	63	1.10E+00	1001	2.07E+00	3.29E+00
0.8	11	64	1.11E+00	1001	2.07E+00	3.28E+00
0.8	13	61	1.11E+00	1001	2.08E+00	3.34E+00
0.8	12	65	1.10E+00	1001	2.08E+00	3.31E+00
0.8	12	65	1.10E+00	1001	2.07E+00	3.33E+00
0.8	10	63	1.10E+00	1001	2.07E+00	3.27E+00
0.8	13	69	1.11E+00	1001	2.08E+00	3.33E+00
0.8	11	64	1.10E+00	1001	2.07E+00	3.28E+00
0.8	11	63	1.10E+00	1001	2.07E+00	3.29E+00
0.8	10	65	1.10E+00	1001	2.07E+00	3.26E+00

0.8	11	65	1.10E+00	1001	2.08E+00	3.33E+00
0.8	10	62	1.10E+00	1001	2.08E+00	3.25E+00
0.8	11	66	1.10E+00	1001	2.07E+00	3.28E+00
0.9	12	64	1.09E+00	1001	2.07E+00	3.33E+00
0.9	10	67	1.10E+00	1001	2.07E+00	3.30E+00
0.9	13	65	1.09E+00	1001	2.08E+00	3.38E+00
0.9	10	64	1.09E+00	1001	2.07E+00	3.31E+00
0.9	10	64	1.09E+00	1001	2.08E+00	3.31E+00
0.9	11	65	1.09E+00	1001	2.07E+00	3.31E+00
0.9	11	65	1.09E+00	1001	2.08E+00	3.30E+00
0.9	10	63	1.09E+00	1001	2.07E+00	3.33E+00
0.9	11	62	1.09E+00	1001	2.08E+00	3.35E+00
0.9	12	66	1.09E+00	1001	2.08E+00	3.36E+00
0.9	11	63	1.09E+00	1001	2.08E+00	3.33E+00
0.9	8	66	1.09E+00	1001	2.07E+00	3.29E+00
0.9	13	64	1.10E+00	1001	2.07E+00	3.35E+00
0.9	11	62	1.09E+00	1001	2.08E+00	3.35E+00
0.9	10	68	1.09E+00	1001	2.08E+00	3.30E+00
0.9	17	60	1.10E+00	1001	2.08E+00	3.45E+00
0.9	9	65	1.09E+00	1001	2.07E+00	3.28E+00
0.9	13	64	1.09E+00	1001	2.08E+00	3.37E+00
0.9	12	65	1.09E+00	1001	2.07E+00	3.31E+00
0.9	14	65	1.09E+00	1001	2.08E+00	3.38E+00
1.0	9	67	1.10E+00	1001	2.07E+00	3.26E+00
1.0	14	63	1.10E+00	1001	2.08E+00	3.36E+00
1.0	12	65	1.10E+00	1001	2.08E+00	3.31E+00
1.0	9	68	1.10E+00	1001	2.07E+00	3.25E+00
1.0	12	61	1.10E+00	1001	2.08E+00	3.31E+00
1.0	8	68	1.10E+00	1001	2.07E+00	3.25E+00
1.0	8	65	1.10E+00	1001	2.07E+00	3.25E+00
1.0	13	67	1.10E+00	1001	2.08E+00	3.35E+00
1.0	8	66	1.10E+00	1001	2.08E+00	3.27E+00
1.0	10	68	1.10E+00	1001	2.07E+00	3.28E+00
1.0	11	66	1.10E+00	1001	2.08E+00	3.30E+00
1.0	9	63	1.10E+00	1001	2.08E+00	3.27E+00
1.0	11	63	1.10E+00	1001	2.07E+00	3.30E+00
1.0	9	68	1.10E+00	1001	2.07E+00	3.27E+00
1.0	12	62	1.10E+00	1001	2.07E+00	3.31E+00
1.0	12	64	1.10E+00	1001	2.07E+00	3.30E+00
1.0	16	63	1.10E+00	1001	2.08E+00	3.40E+00
1.0	10	66	1.10E+00	1001	2.08E+00	3.28E+00
1.0	11	66	1.10E+00	1001	2.07E+00	3.28E+00
1.0	10	64	1.10E+00	1001	2.07E+00	3.27E+00

Experiment 5.7.2

Movement probability	Average cooperation	Average relatedness	Average interaction length	Model time	Average cell population	Average number of partners
0.0	82	95	2.20E+00	1001	3.97E+00	1.91E+00
0.0	67	95	2.04E+00	869	3.86E+00	1.87E+00
0.0	73	97	2.07E+00	1001	3.92E+00	1.91E+00
0.0	35	94	1.74E+00	507	3.68E+00	1.87E+00
0.0	73	94	2.36E+00	800	4.05E+00	1.89E+00
0.0	65	96	2.16E+00	1001	3.87E+00	1.87E+00
0.0	29	95	1.88E+00	762	3.70E+00	1.90E+00
0.0	63	96	2.23E+00	579	3.92E+00	1.84E+00
0.0	59	94	2.07E+00	858	3.88E+00	1.84E+00
0.0	52	95	1.92E+00	636	3.78E+00	1.86E+00
0.0	71	95	2.48E+00	978	3.98E+00	1.83E+00

0.0	60	96	2.16E+00	1001	3.95E+00	1.90E+00
0.0	84	96	2.15E+00	1001	3.94E+00	1.88E+00
0.0	61	95	2.25E+00	1001	4.00E+00	1.89E+00
0.0	86	96	2.35E+00	989	3.94E+00	1.87E+00
0.0	70	95	2.11E+00	995	3.90E+00	1.86E+00
0.0	71	96	2.09E+00	1001	3.94E+00	1.93E+00
0.0	80	95	2.56E+00	974	4.14E+00	1.93E+00
0.0	75	95	2.14E+00	780	3.95E+00	1.94E+00
0.0	85	96	2.34E+00	1001	3.94E+00	1.84E+00
0.1	25	78	1.57E+00	1001	3.29E+00	1.90E+00
0.1	32	79	1.62E+00	1001	3.39E+00	1.95E+00
0.1	32	75	1.63E+00	1001	3.48E+00	1.99E+00
0.1	33	78	1.65E+00	1001	3.51E+00	2.02E+00
0.1	31	76	1.62E+00	1001	3.46E+00	1.98E+00
0.1	30	77	1.61E+00	1001	3.40E+00	1.97E+00
0.1	34	75	1.65E+00	1001	3.50E+00	2.01E+00
0.1	28	78	1.59E+00	1001	3.40E+00	1.95E+00
0.1	30	77	1.61E+00	1001	3.38E+00	1.95E+00
0.1	27	78	1.58E+00	1001	3.32E+00	1.91E+00
0.1	23	77	1.55E+00	1001	3.25E+00	1.88E+00
0.1	26	78	1.57E+00	1001	3.38E+00	1.94E+00
0.1	31	78	1.61E+00	1001	3.45E+00	1.98E+00
0.1	22	79	1.55E+00	1001	3.25E+00	1.88E+00
0.1	31	77	1.62E+00	1001	3.41E+00	1.98E+00
0.1	32	76	1.63E+00	1001	3.50E+00	2.00E+00
0.1	31	77	1.61E+00	1001	3.42E+00	1.97E+00
0.1	25	79	1.55E+00	1001	3.30E+00	1.91E+00
0.1	27	78	1.58E+00	1001	3.35E+00	1.94E+00
0.1	28	76	1.59E+00	1001	3.36E+00	1.94E+00
0.2	14	71	1.38E+00	1001	3.24E+00	2.01E+00
0.2	13	72	1.38E+00	1001	3.18E+00	1.98E+00
0.2	13	71	1.38E+00	1001	3.19E+00	1.99E+00
0.2	12	72	1.37E+00	1001	3.17E+00	1.98E+00
0.2	13	73	1.38E+00	1001	3.16E+00	1.97E+00
0.2	10	75	1.37E+00	1001	3.13E+00	1.93E+00
0.2	12	74	1.37E+00	1001	3.16E+00	1.97E+00
0.2	14	72	1.38E+00	1001	3.21E+00	1.99E+00
0.2	14	72	1.39E+00	1001	3.20E+00	1.99E+00
0.2	14	72	1.39E+00	1001	3.23E+00	2.00E+00
0.2	12	73	1.38E+00	1001	3.18E+00	1.98E+00
0.2	13	73	1.38E+00	1001	3.18E+00	1.98E+00
0.2	13	72	1.38E+00	1001	3.19E+00	1.98E+00
0.2	13	71	1.38E+00	1001	3.20E+00	1.99E+00
0.2	15	71	1.39E+00	1001	3.24E+00	2.02E+00
0.2	17	71	1.40E+00	1001	3.27E+00	2.03E+00
0.2	14	72	1.39E+00	1001	3.22E+00	2.01E+00
0.2	15	71	1.39E+00	1001	3.24E+00	2.01E+00
0.2	13	73	1.38E+00	1001	3.18E+00	1.98E+00
0.2	14	71	1.38E+00	1001	3.18E+00	1.98E+00
0.3	8	71	1.27E+00	1001	3.10E+00	2.06E+00
0.3	10	70	1.27E+00	1001	3.15E+00	2.11E+00
0.3	7	71	1.27E+00	1001	3.09E+00	2.04E+00
0.3	10	69	1.27E+00	1001	3.15E+00	2.10E+00
0.3	10	69	1.27E+00	1001	3.16E+00	2.11E+00
0.3	9	70	1.27E+00	1001	3.14E+00	2.08E+00
0.3	9	70	1.27E+00	1001	3.12E+00	2.08E+00
0.3	10	71	1.27E+00	1001	3.14E+00	2.10E+00
0.3	9	69	1.27E+00	1001	3.12E+00	2.07E+00

0.3	9	71	1.27E+00	1001	3.12E+00	2.08E+00
0.3	8	72	1.27E+00	1001	3.12E+00	2.08E+00
0.3	8	71	1.27E+00	1001	3.12E+00	2.07E+00
0.3	9	70	1.27E+00	1001	3.12E+00	2.08E+00
0.3	9	70	1.28E+00	1001	3.14E+00	2.09E+00
0.3	8	72	1.27E+00	1001	3.10E+00	2.06E+00
0.3	10	69	1.27E+00	1001	3.12E+00	2.08E+00
0.3	9	70	1.27E+00	1001	3.11E+00	2.07E+00
0.3	10	69	1.27E+00	1001	3.14E+00	2.10E+00
0.3	10	69	1.27E+00	1001	3.14E+00	2.09E+00
0.3	12	67	1.28E+00	1001	3.18E+00	2.14E+00
0.4	8	67	1.20E+00	1001	3.08E+00	2.18E+00
0.4	7	68	1.20E+00	1001	3.09E+00	2.17E+00
0.4	7	67	1.19E+00	1001	3.10E+00	2.18E+00
0.4	7	68	1.19E+00	1001	3.07E+00	2.17E+00
0.4	9	66	1.20E+00	1001	3.14E+00	2.21E+00
0.4	7	69	1.19E+00	1001	3.07E+00	2.17E+00
0.4	8	67	1.20E+00	1001	3.09E+00	2.19E+00
0.4	6	69	1.19E+00	1001	3.08E+00	2.16E+00
0.4	7	68	1.19E+00	1001	3.11E+00	2.19E+00
0.4	8	67	1.20E+00	1001	3.10E+00	2.19E+00
0.4	9	67	1.20E+00	1001	3.10E+00	2.20E+00
0.4	8	68	1.19E+00	1001	3.10E+00	2.19E+00
0.4	6	68	1.19E+00	1001	3.10E+00	2.17E+00
0.4	6	70	1.19E+00	1001	3.04E+00	2.15E+00
0.4	8	68	1.19E+00	1001	3.09E+00	2.19E+00
0.4	9	68	1.19E+00	1001	3.11E+00	2.20E+00
0.4	8	68	1.20E+00	1001	3.12E+00	2.20E+00
0.4	7	68	1.20E+00	1001	3.05E+00	2.15E+00
0.4	8	68	1.19E+00	1001	3.11E+00	2.20E+00
0.4	8	67	1.19E+00	1001	3.09E+00	2.19E+00
0.5	6	66	1.14E+00	1001	3.09E+00	2.28E+00
0.5	5	66	1.14E+00	1001	3.04E+00	2.23E+00
0.5	6	69	1.14E+00	1001	3.06E+00	2.26E+00
0.5	7	67	1.14E+00	1001	3.09E+00	2.29E+00
0.5	6	65	1.14E+00	1001	3.06E+00	2.25E+00
0.5	6	67	1.14E+00	1001	3.05E+00	2.26E+00
0.5	6	65	1.13E+00	1001	3.06E+00	2.26E+00
0.5	7	65	1.14E+00	1001	3.10E+00	2.29E+00
0.5	6	67	1.14E+00	1001	3.05E+00	2.25E+00
0.5	7	67	1.14E+00	1001	3.07E+00	2.27E+00
0.5	6	67	1.14E+00	1001	3.06E+00	2.25E+00
0.5	6	69	1.14E+00	1001	3.04E+00	2.24E+00
0.5	6	67	1.14E+00	1001	3.06E+00	2.26E+00
0.5	6	66	1.14E+00	1001	3.06E+00	2.26E+00
0.5	6	66	1.14E+00	1001	3.06E+00	2.26E+00
0.5	7	65	1.14E+00	1001	3.08E+00	2.27E+00
0.5	5	69	1.14E+00	1001	3.05E+00	2.25E+00
0.5	6	67	1.14E+00	1001	3.05E+00	2.25E+00
0.5	6	65	1.14E+00	1001	3.08E+00	2.27E+00
0.5	8	67	1.14E+00	1001	3.09E+00	2.29E+00
0.6	4	66	1.10E+00	1001	3.04E+00	2.31E+00
0.6	4	66	1.10E+00	1001	3.01E+00	2.30E+00
0.6	5	65	1.10E+00	1001	3.04E+00	2.31E+00
0.6	5	65	1.10E+00	1001	3.04E+00	2.31E+00
0.6	4	65	1.09E+00	1001	3.02E+00	2.31E+00
0.6	5	67	1.10E+00	1001	3.02E+00	2.31E+00
0.6	4	66	1.09E+00	1001	3.03E+00	2.31E+00

0.6	5	65	1.10E+00	1001	3.04E+00	2.32E+00
0.6	5	66	1.10E+00	1001	3.00E+00	2.30E+00
0.6	5	66	1.10E+00	1001	3.05E+00	2.33E+00
0.6	5	66	1.10E+00	1001	3.04E+00	2.32E+00
0.6	5	66	1.10E+00	1001	3.04E+00	2.32E+00
0.6	5	64	1.10E+00	1001	3.05E+00	2.32E+00
0.6	5	66	1.10E+00	1001	3.03E+00	2.32E+00
0.6	4	65	1.10E+00	1001	3.03E+00	2.31E+00
0.6	5	66	1.10E+00	1001	3.05E+00	2.32E+00
0.6	5	65	1.10E+00	1001	3.03E+00	2.32E+00
0.6	6	64	1.09E+00	1001	3.05E+00	2.33E+00
0.6	5	64	1.10E+00	1001	3.03E+00	2.31E+00
0.6	5	66	1.10E+00	1001	3.03E+00	2.30E+00
0.7	4	64	1.07E+00	1001	3.01E+00	2.35E+00
0.7	4	64	1.07E+00	1001	3.01E+00	2.34E+00
0.7	4	65	1.07E+00	1001	3.02E+00	2.36E+00
0.7	5	63	1.07E+00	1001	3.04E+00	2.38E+00
0.7	5	65	1.07E+00	1001	3.01E+00	2.36E+00
0.7	4	67	1.07E+00	1001	3.00E+00	2.33E+00
0.7	4	66	1.07E+00	1001	3.01E+00	2.35E+00
0.7	5	65	1.07E+00	1001	3.01E+00	2.36E+00
0.7	4	63	1.07E+00	1001	3.02E+00	2.35E+00
0.7	5	64	1.07E+00	1001	3.03E+00	2.37E+00
0.7	4	65	1.07E+00	1001	3.01E+00	2.34E+00
0.7	4	63	1.07E+00	1001	3.03E+00	2.36E+00
0.7	4	63	1.07E+00	1001	3.03E+00	2.35E+00
0.7	4	66	1.07E+00	1001	3.02E+00	2.35E+00
0.7	4	66	1.07E+00	1001	3.01E+00	2.35E+00
0.7	3	65	1.07E+00	1001	3.01E+00	2.34E+00
0.7	4	64	1.07E+00	1001	3.03E+00	2.36E+00
0.7	5	63	1.07E+00	1001	3.03E+00	2.36E+00
0.7	4	64	1.07E+00	1001	3.02E+00	2.36E+00
0.7	5	66	1.07E+00	1001	3.03E+00	2.37E+00
0.8	4	64	1.06E+00	1001	3.02E+00	2.39E+00
0.8	3	66	1.05E+00	1001	3.01E+00	2.37E+00
0.8	4	64	1.05E+00	1001	3.01E+00	2.38E+00
0.8	4	62	1.05E+00	1001	3.02E+00	2.39E+00
0.8	5	64	1.06E+00	1001	3.04E+00	2.41E+00
0.8	4	64	1.05E+00	1001	3.01E+00	2.38E+00
0.8	3	64	1.06E+00	1001	3.02E+00	2.37E+00
0.8	5	63	1.06E+00	1001	3.02E+00	2.40E+00
0.8	4	64	1.05E+00	1001	3.00E+00	2.37E+00
0.8	3	64	1.06E+00	1001	3.01E+00	2.37E+00
0.8	4	65	1.06E+00	1001	3.01E+00	2.37E+00
0.8	4	64	1.05E+00	1001	3.01E+00	2.38E+00
0.8	4	65	1.05E+00	1001	3.02E+00	2.37E+00
0.8	4	64	1.05E+00	1001	3.02E+00	2.38E+00
0.8	4	64	1.06E+00	1001	3.01E+00	2.38E+00
0.8	4	64	1.05E+00	1001	2.99E+00	2.37E+00
0.8	5	62	1.05E+00	1001	3.03E+00	2.40E+00
0.8	3	63	1.05E+00	1001	3.00E+00	2.36E+00
0.8	4	64	1.05E+00	1001	3.00E+00	2.37E+00
0.8	4	62	1.06E+00	1001	3.03E+00	2.41E+00
0.9	4	65	1.05E+00	1001	3.01E+00	2.39E+00
0.9	3	64	1.05E+00	1001	3.00E+00	2.36E+00
0.9	3	62	1.05E+00	1001	3.00E+00	2.39E+00
0.9	4	62	1.05E+00	1001	3.02E+00	2.39E+00
0.9	4	63	1.05E+00	1001	3.00E+00	2.39E+00

0.9	4	64	1.05E+00	1001	3.01E+00	2.38E+00
0.9	4	64	1.05E+00	1001	3.02E+00	2.39E+00
0.9	4	63	1.05E+00	1001	2.99E+00	2.37E+00
0.9	4	62	1.05E+00	1001	2.99E+00	2.37E+00
0.9	4	62	1.05E+00	1001	3.00E+00	2.38E+00
0.9	4	64	1.05E+00	1001	3.04E+00	2.42E+00
0.9	4	65	1.05E+00	1001	3.00E+00	2.37E+00
0.9	4	63	1.05E+00	1001	3.01E+00	2.39E+00
0.9	4	62	1.05E+00	1001	3.01E+00	2.38E+00
0.9	4	63	1.05E+00	1001	3.01E+00	2.38E+00
0.9	4	65	1.05E+00	1001	3.01E+00	2.40E+00
0.9	3	64	1.05E+00	1001	2.97E+00	2.36E+00
0.9	4	63	1.05E+00	1001	3.02E+00	2.39E+00
0.9	4	63	1.05E+00	1001	3.00E+00	2.39E+00
0.9	4	63	1.05E+00	1001	3.01E+00	2.38E+00
1.0	3	64	1.06E+00	1001	3.01E+00	2.35E+00
1.0	3	65	1.06E+00	1001	3.00E+00	2.35E+00
1.0	4	63	1.06E+00	1001	3.01E+00	2.36E+00
1.0	4	63	1.06E+00	1001	3.01E+00	2.36E+00
1.0	4	64	1.06E+00	1001	2.99E+00	2.36E+00
1.0	4	63	1.06E+00	1001	3.01E+00	2.36E+00
1.0	3	64	1.06E+00	1001	3.00E+00	2.35E+00
1.0	4	63	1.06E+00	1001	3.01E+00	2.37E+00
1.0	4	65	1.06E+00	1001	2.99E+00	2.36E+00
1.0	3	64	1.06E+00	1001	3.01E+00	2.35E+00
1.0	4	64	1.06E+00	1001	3.00E+00	2.37E+00
1.0	3	63	1.06E+00	1001	3.01E+00	2.36E+00
1.0	4	64	1.06E+00	1001	3.01E+00	2.36E+00
1.0	4	63	1.06E+00	1001	3.00E+00	2.36E+00
1.0	4	65	1.06E+00	1001	3.03E+00	2.38E+00
1.0	3	65	1.06E+00	1001	2.98E+00	2.34E+00
1.0	4	62	1.06E+00	1001	3.03E+00	2.38E+00
1.0	3	63	1.06E+00	1001	2.99E+00	2.35E+00
1.0	4	67	1.06E+00	1001	3.00E+00	2.36E+00
1.0	5	65	1.06E+00	1001	3.02E+00	2.38E+00

Experiment 5.7.3

Movement probability	Average cooperation	Average relatedness	Average interaction length	Model time	Average cell population	Average number of partners
0.0	43	96	0.00E+00	1001	3.98E+00	0.00E+00
0.0	66	97	0.00E+00	948	4.11E+00	0.00E+00
0.0	67	97	0.00E+00	1001	4.02E+00	0.00E+00
0.0	59	96	0.00E+00	1001	4.05E+00	0.00E+00
0.0	61	96	0.00E+00	923	3.98E+00	0.00E+00
0.0	43	95	0.00E+00	765	3.82E+00	0.00E+00
0.0	72	97	0.00E+00	1001	4.11E+00	0.00E+00
0.0	60	97	0.00E+00	1001	4.06E+00	0.00E+00
0.0	68	97	0.00E+00	1001	4.09E+00	0.00E+00
0.0	59	94	0.00E+00	1001	4.04E+00	0.00E+00
0.0	35	96	0.00E+00	613	3.80E+00	0.00E+00
0.0	58	96	0.00E+00	1001	4.07E+00	0.00E+00
0.0	57	92	0.00E+00	422	3.82E+00	0.00E+00
0.0	68	94	0.00E+00	670	4.02E+00	0.00E+00
0.0	53	95	0.00E+00	1001	3.94E+00	0.00E+00
0.0	51	96	0.00E+00	998	3.98E+00	0.00E+00
0.0	43	93	0.00E+00	751	3.90E+00	0.00E+00
0.0	71	96	0.00E+00	1001	4.03E+00	0.00E+00
0.0	72	96	0.00E+00	720	3.92E+00	0.00E+00

0.0	58	96	0.00E+00	1001	4.08E+00	0.00E+00
0.1	28	80	0.00E+00	1001	3.46E+00	0.00E+00
0.1	24	80	0.00E+00	1001	3.38E+00	0.00E+00
0.1	23	81	0.00E+00	1001	3.34E+00	0.00E+00
0.1	23	80	0.00E+00	1001	3.36E+00	0.00E+00
0.1	23	81	0.00E+00	1001	3.33E+00	0.00E+00
0.1	25	80	0.00E+00	1001	3.35E+00	0.00E+00
0.1	24	80	0.00E+00	1001	3.38E+00	0.00E+00
0.1	27	79	0.00E+00	1001	3.44E+00	0.00E+00
0.1	23	81	0.00E+00	1001	3.34E+00	0.00E+00
0.1	25	81	0.00E+00	1001	3.41E+00	0.00E+00
0.1	25	79	0.00E+00	1001	3.40E+00	0.00E+00
0.1	23	80	0.00E+00	1001	3.36E+00	0.00E+00
0.1	25	80	0.00E+00	1001	3.44E+00	0.00E+00
0.1	27	78	0.00E+00	1001	3.40E+00	0.00E+00
0.1	24	80	0.00E+00	1001	3.34E+00	0.00E+00
0.1	27	80	0.00E+00	1001	3.43E+00	0.00E+00
0.1	24	81	0.00E+00	1001	3.40E+00	0.00E+00
0.1	26	80	0.00E+00	1001	3.41E+00	0.00E+00
0.1	24	80	0.00E+00	1001	3.39E+00	0.00E+00
0.1	23	81	0.00E+00	1001	3.38E+00	0.00E+00
0.2	12	83	0.00E+00	1001	3.19E+00	0.00E+00
0.2	11	84	0.00E+00	1001	3.14E+00	0.00E+00
0.2	11	85	0.00E+00	1001	3.17E+00	0.00E+00
0.2	13	83	0.00E+00	1001	3.21E+00	0.00E+00
0.2	12	84	0.00E+00	1001	3.18E+00	0.00E+00
0.2	10	85	0.00E+00	1001	3.17E+00	0.00E+00
0.2	9	86	0.00E+00	1001	3.13E+00	0.00E+00
0.2	12	84	0.00E+00	1001	3.20E+00	0.00E+00
0.2	12	82	0.00E+00	1001	3.21E+00	0.00E+00
0.2	12	84	0.00E+00	1001	3.15E+00	0.00E+00
0.2	13	82	0.00E+00	1001	3.25E+00	0.00E+00
0.2	11	84	0.00E+00	1001	3.19E+00	0.00E+00
0.2	13	83	0.00E+00	1001	3.21E+00	0.00E+00
0.2	13	83	0.00E+00	1001	3.23E+00	0.00E+00
0.2	11	84	0.00E+00	1001	3.17E+00	0.00E+00
0.2	13	83	0.00E+00	1001	3.19E+00	0.00E+00
0.2	13	83	0.00E+00	1001	3.21E+00	0.00E+00
0.2	12	83	0.00E+00	1001	3.20E+00	0.00E+00
0.2	11	84	0.00E+00	1001	3.19E+00	0.00E+00
0.2	11	85	0.00E+00	1001	3.18E+00	0.00E+00
0.3	7	87	0.00E+00	1001	3.10E+00	0.00E+00
0.3	9	85	0.00E+00	1001	3.13E+00	0.00E+00
0.3	10	84	0.00E+00	1001	3.17E+00	0.00E+00
0.3	9	85	0.00E+00	1001	3.16E+00	0.00E+00
0.3	8	86	0.00E+00	1001	3.12E+00	0.00E+00
0.3	8	85	0.00E+00	1001	3.12E+00	0.00E+00
0.3	10	84	0.00E+00	1001	3.14E+00	0.00E+00
0.3	9	85	0.00E+00	1001	3.14E+00	0.00E+00
0.3	8	85	0.00E+00	1001	3.12E+00	0.00E+00
0.3	9	85	0.00E+00	1001	3.13E+00	0.00E+00
0.3	10	85	0.00E+00	1001	3.14E+00	0.00E+00
0.3	10	84	0.00E+00	1001	3.17E+00	0.00E+00
0.3	8	86	0.00E+00	1001	3.13E+00	0.00E+00
0.3	10	84	0.00E+00	1001	3.15E+00	0.00E+00
0.3	8	86	0.00E+00	1001	3.14E+00	0.00E+00
0.3	10	85	0.00E+00	1001	3.14E+00	0.00E+00
0.3	9	85	0.00E+00	1001	3.14E+00	0.00E+00

0.3	9	86	0.00E+00	1001	3.13E+00	0.00E+00
0.3	10	84	0.00E+00	1001	3.14E+00	0.00E+00
0.3	8	87	0.00E+00	1001	3.10E+00	0.00E+00
0.4	7	87	0.00E+00	1001	3.11E+00	0.00E+00
0.4	7	86	0.00E+00	1001	3.10E+00	0.00E+00
0.4	7	86	0.00E+00	1001	3.12E+00	0.00E+00
0.4	7	87	0.00E+00	1001	3.08E+00	0.00E+00
0.4	9	84	0.00E+00	1001	3.11E+00	0.00E+00
0.4	8	86	0.00E+00	1001	3.12E+00	0.00E+00
0.4	7	87	0.00E+00	1001	3.07E+00	0.00E+00
0.4	7	86	0.00E+00	1001	3.10E+00	0.00E+00
0.4	8	86	0.00E+00	1001	3.12E+00	0.00E+00
0.4	8	85	0.00E+00	1001	3.10E+00	0.00E+00
0.4	8	86	0.00E+00	1001	3.11E+00	0.00E+00
0.4	8	87	0.00E+00	1001	3.09E+00	0.00E+00
0.4	7	87	0.00E+00	1001	3.10E+00	0.00E+00
0.4	9	85	0.00E+00	1001	3.13E+00	0.00E+00
0.4	7	86	0.00E+00	1001	3.10E+00	0.00E+00
0.4	7	86	0.00E+00	1001	3.10E+00	0.00E+00
0.4	7	87	0.00E+00	1001	3.08E+00	0.00E+00
0.4	7	86	0.00E+00	1001	3.10E+00	0.00E+00
0.4	8	85	0.00E+00	1001	3.11E+00	0.00E+00
0.4	7	87	0.00E+00	1001	3.08E+00	0.00E+00
0.5	6	88	0.00E+00	1001	3.08E+00	0.00E+00
0.5	7	86	0.00E+00	1001	3.09E+00	0.00E+00
0.5	7	86	0.00E+00	1001	3.08E+00	0.00E+00
0.5	6	88	0.00E+00	1001	3.07E+00	0.00E+00
0.5	6	87	0.00E+00	1001	3.07E+00	0.00E+00
0.5	7	86	0.00E+00	1001	3.11E+00	0.00E+00
0.5	7	86	0.00E+00	1001	3.08E+00	0.00E+00
0.5	7	87	0.00E+00	1001	3.09E+00	0.00E+00
0.5	7	86	0.00E+00	1001	3.09E+00	0.00E+00
0.5	7	86	0.00E+00	1001	3.08E+00	0.00E+00
0.5	6	87	0.00E+00	1001	3.07E+00	0.00E+00
0.5	6	87	0.00E+00	1001	3.07E+00	0.00E+00
0.5	7	86	0.00E+00	1001	3.09E+00	0.00E+00
0.5	8	86	0.00E+00	1001	3.09E+00	0.00E+00
0.5	7	86	0.00E+00	1001	3.11E+00	0.00E+00
0.5	7	87	0.00E+00	1001	3.11E+00	0.00E+00
0.5	7	87	0.00E+00	1001	3.09E+00	0.00E+00
0.5	8	86	0.00E+00	1001	3.10E+00	0.00E+00
0.5	7	86	0.00E+00	1001	3.10E+00	0.00E+00
0.5	6	88	0.00E+00	1001	3.06E+00	0.00E+00
0.6	7	87	0.00E+00	1001	3.09E+00	0.00E+00
0.6	6	87	0.00E+00	1001	3.07E+00	0.00E+00
0.6	6	88	0.00E+00	1001	3.07E+00	0.00E+00
0.6	6	88	0.00E+00	1001	3.05E+00	0.00E+00
0.6	7	87	0.00E+00	1001	3.10E+00	0.00E+00
0.6	6	87	0.00E+00	1001	3.10E+00	0.00E+00
0.6	6	87	0.00E+00	1001	3.06E+00	0.00E+00
0.6	7	86	0.00E+00	1001	3.07E+00	0.00E+00
0.6	6	87	0.00E+00	1001	3.07E+00	0.00E+00
0.6	7	86	0.00E+00	1001	3.08E+00	0.00E+00
0.6	6	88	0.00E+00	1001	3.06E+00	0.00E+00
0.6	6	87	0.00E+00	1001	3.09E+00	0.00E+00
0.6	7	87	0.00E+00	1001	3.09E+00	0.00E+00
0.6	6	88	0.00E+00	1001	3.06E+00	0.00E+00
0.6	7	86	0.00E+00	1001	3.08E+00	0.00E+00

0.6	6	88	0.00E+00	1001	3.07E+00	0.00E+00
0.6	7	87	0.00E+00	1001	3.10E+00	0.00E+00
0.6	5	89	0.00E+00	1001	3.05E+00	0.00E+00
0.6	6	88	0.00E+00	1001	3.06E+00	0.00E+00
0.6	6	87	0.00E+00	1001	3.08E+00	0.00E+00
0.7	5	88	0.00E+00	1001	3.07E+00	0.00E+00
0.7	6	88	0.00E+00	1001	3.06E+00	0.00E+00
0.7	5	88	0.00E+00	1001	3.05E+00	0.00E+00
0.7	6	87	0.00E+00	1001	3.08E+00	0.00E+00
0.7	6	88	0.00E+00	1001	3.04E+00	0.00E+00
0.7	6	88	0.00E+00	1001	3.05E+00	0.00E+00
0.7	6	88	0.00E+00	1001	3.07E+00	0.00E+00
0.7	5	88	0.00E+00	1001	3.03E+00	0.00E+00
0.7	6	87	0.00E+00	1001	3.07E+00	0.00E+00
0.7	5	89	0.00E+00	1001	3.05E+00	0.00E+00
0.7	5	89	0.00E+00	1001	3.02E+00	0.00E+00
0.7	7	86	0.00E+00	1001	3.09E+00	0.00E+00
0.7	6	88	0.00E+00	1001	3.07E+00	0.00E+00
0.7	5	88	0.00E+00	1001	3.05E+00	0.00E+00
0.7	6	87	0.00E+00	1001	3.08E+00	0.00E+00
0.7	5	89	0.00E+00	1001	3.05E+00	0.00E+00
0.7	6	87	0.00E+00	1001	3.08E+00	0.00E+00
0.7	7	87	0.00E+00	1001	3.09E+00	0.00E+00
0.7	5	89	0.00E+00	1001	3.03E+00	0.00E+00
0.7	6	88	0.00E+00	1001	3.08E+00	0.00E+00
0.8	5	88	0.00E+00	1001	3.05E+00	0.00E+00
0.8	6	88	0.00E+00	1001	3.06E+00	0.00E+00
0.8	5	88	0.00E+00	1001	3.05E+00	0.00E+00
0.8	6	88	0.00E+00	1001	3.06E+00	0.00E+00
0.8	6	88	0.00E+00	1001	3.05E+00	0.00E+00
0.8	5	89	0.00E+00	1001	3.05E+00	0.00E+00
0.8	5	88	0.00E+00	1001	3.05E+00	0.00E+00
0.8	5	88	0.00E+00	1001	3.05E+00	0.00E+00
0.8	6	89	0.00E+00	1001	3.06E+00	0.00E+00
0.8	6	88	0.00E+00	1001	3.05E+00	0.00E+00
0.8	5	88	0.00E+00	1001	3.07E+00	0.00E+00
0.8	6	87	0.00E+00	1001	3.07E+00	0.00E+00
0.8	5	88	0.00E+00	1001	3.05E+00	0.00E+00
0.8	6	88	0.00E+00	1001	3.07E+00	0.00E+00
0.8	6	87	0.00E+00	1001	3.06E+00	0.00E+00
0.8	6	88	0.00E+00	1001	3.07E+00	0.00E+00
0.8	5	89	0.00E+00	1001	3.03E+00	0.00E+00
0.8	5	89	0.00E+00	1001	3.05E+00	0.00E+00
0.8	6	87	0.00E+00	1001	3.06E+00	0.00E+00
0.8	6	88	0.00E+00	1001	3.05E+00	0.00E+00
0.9	4	90	0.00E+00	1001	3.03E+00	0.00E+00
0.9	6	88	0.00E+00	1001	3.07E+00	0.00E+00
0.9	5	89	0.00E+00	1001	3.04E+00	0.00E+00
0.9	6	88	0.00E+00	1001	3.05E+00	0.00E+00
0.9	5	88	0.00E+00	1001	3.06E+00	0.00E+00
0.9	5	89	0.00E+00	1001	3.05E+00	0.00E+00
0.9	5	88	0.00E+00	1001	3.04E+00	0.00E+00
0.9	6	88	0.00E+00	1001	3.04E+00	0.00E+00
0.9	5	89	0.00E+00	1001	3.03E+00	0.00E+00
0.9	5	88	0.00E+00	1001	3.06E+00	0.00E+00
0.9	5	89	0.00E+00	1001	3.04E+00	0.00E+00
0.9	5	88	0.00E+00	1001	3.04E+00	0.00E+00
0.9	6	87	0.00E+00	1001	3.06E+00	0.00E+00

0.9	6	87	0.00E+00	1001	3.08E+00	0.00E+00
0.9	6	88	0.00E+00	1001	3.06E+00	0.00E+00
0.9	6	88	0.00E+00	1001	3.06E+00	0.00E+00
0.9	5	89	0.00E+00	1001	3.05E+00	0.00E+00
0.9	6	88	0.00E+00	1001	3.06E+00	0.00E+00
0.9	5	88	0.00E+00	1001	3.04E+00	0.00E+00
0.9	5	89	0.00E+00	1001	3.05E+00	0.00E+00
1.0	6	88	0.00E+00	1001	3.07E+00	0.00E+00
1.0	5	89	0.00E+00	1001	3.03E+00	0.00E+00
1.0	5	89	0.00E+00	1001	3.04E+00	0.00E+00
1.0	6	89	0.00E+00	1001	3.08E+00	0.00E+00
1.0	5	90	0.00E+00	1001	3.03E+00	0.00E+00
1.0	5	89	0.00E+00	1001	3.04E+00	0.00E+00
1.0	6	88	0.00E+00	1001	3.05E+00	0.00E+00
1.0	4	90	0.00E+00	1001	3.02E+00	0.00E+00
1.0	5	89	0.00E+00	1001	3.03E+00	0.00E+00
1.0	5	89	0.00E+00	1001	3.06E+00	0.00E+00
1.0	6	88	0.00E+00	1001	3.05E+00	0.00E+00
1.0	5	89	0.00E+00	1001	3.04E+00	0.00E+00
1.0	7	87	0.00E+00	1001	3.09E+00	0.00E+00
1.0	6	88	0.00E+00	1001	3.06E+00	0.00E+00
1.0	5	89	0.00E+00	1001	3.05E+00	0.00E+00
1.0	6	88	0.00E+00	1001	3.06E+00	0.00E+00
1.0	6	87	0.00E+00	1001	3.07E+00	0.00E+00
1.0	5	89	0.00E+00	1001	3.04E+00	0.00E+00
1.0	6	88	0.00E+00	1001	3.05E+00	0.00E+00
1.0	7	87	0.00E+00	1001	3.09E+00	0.00E+00

Experiment 5.8.1

Movement probability	Average cooperation	Average relatedness	Average interaction length	Model time	Average cell population	Average number of partners
0.0	84	75	1.10E+00	1001	4.26E+01	8.12E+00
0.0	77	64	1.02E+00	1001	8.32E+01	8.79E+00
0.0	47	68	1.03E+00	1001	6.04E+01	4.73E+00
0.0	79	73	1.05E+00	1001	5.76E+01	7.94E+00
0.0	82	76	1.11E+00	1001	4.12E+01	7.68E+00
0.0	83	68	1.08E+00	1001	4.66E+01	8.26E+00
0.0	81	72	1.06E+00	1001	5.94E+01	8.47E+00
0.0	87	73	1.06E+00	1001	5.47E+01	8.40E+00
0.0	77	70	1.06E+00	1001	5.80E+01	8.30E+00
0.0	81	69	1.04E+00	1001	6.39E+01	8.54E+00
0.0	57	70	1.02E+00	1001	7.53E+01	5.57E+00
0.0	63	72	1.04E+00	1001	5.93E+01	6.09E+00
0.0	47	72	1.04E+00	1001	5.82E+01	4.69E+00
0.0	58	74	1.04E+00	1001	6.34E+01	5.61E+00
0.0	61	70	1.02E+00	1001	7.58E+01	6.08E+00
0.0	86	77	1.07E+00	1001	4.98E+01	8.30E+00
0.0	55	71	1.06E+00	1001	5.15E+01	5.21E+00
0.0	84	81	1.11E+00	1001	3.67E+01	7.75E+00
0.0	84	74	1.06E+00	1001	5.68E+01	8.26E+00
0.0	72	78	1.07E+00	1001	4.98E+01	6.95E+00
0.1	63	71	1.71E+00	1001	4.34E+00	3.25E+00
0.1	86	73	2.00E+00	1001	3.51E+00	3.17E+00
0.1	75	69	1.93E+00	1001	3.69E+00	3.14E+00
0.1	86	75	2.05E+00	1001	3.37E+00	3.06E+00
0.1	74	69	1.87E+00	1001	3.68E+00	3.09E+00
0.1	68	71	1.80E+00	1001	4.03E+00	3.20E+00
0.1	74	74	1.90E+00	1001	3.71E+00	3.16E+00

0.1	77	73	1.90E+00	1001	3.86E+00	3.25E+00
0.1	75	69	1.88E+00	1001	3.86E+00	3.22E+00
0.1	68	73	1.80E+00	1001	4.02E+00	3.18E+00
0.1	77	73	1.91E+00	1001	3.67E+00	3.11E+00
0.1	75	69	1.91E+00	1001	3.54E+00	3.02E+00
0.1	84	74	2.04E+00	1001	3.25E+00	2.95E+00
0.1	74	74	1.83E+00	1001	3.78E+00	3.12E+00
0.1	87	74	2.05E+00	1001	3.37E+00	3.09E+00
0.1	80	76	1.99E+00	1001	3.32E+00	2.91E+00
0.1	73	68	1.86E+00	1001	3.87E+00	3.18E+00
0.1	69	73	1.82E+00	1001	3.97E+00	3.18E+00
0.1	84	72	2.01E+00	1001	3.43E+00	3.15E+00
0.1	86	74	2.01E+00	1001	3.49E+00	3.14E+00
0.2	73	70	1.69E+00	1001	2.87E+00	3.13E+00
0.2	63	70	1.62E+00	1001	3.08E+00	3.06E+00
0.2	67	68	1.62E+00	1001	2.90E+00	2.91E+00
0.2	83	70	1.76E+00	1001	2.73E+00	3.23E+00
0.2	71	66	1.66E+00	1001	2.94E+00	3.08E+00
0.2	69	72	1.64E+00	1001	3.04E+00	3.15E+00
0.2	47	67	1.47E+00	1001	3.06E+00	2.51E+00
0.2	61	65	1.56E+00	1001	3.00E+00	2.82E+00
0.2	71	69	1.66E+00	1001	2.90E+00	3.08E+00
0.2	78	70	1.74E+00	1001	2.74E+00	3.13E+00
0.2	78	75	1.67E+00	1001	2.84E+00	3.09E+00
0.2	66	69	1.62E+00	1001	3.08E+00	3.13E+00
0.2	84	74	1.76E+00	1001	2.73E+00	3.30E+00
0.2	76	64	1.69E+00	1001	2.86E+00	3.16E+00
0.2	72	65	1.66E+00	1001	2.95E+00	3.15E+00
0.2	80	68	1.73E+00	1001	2.81E+00	3.26E+00
0.2	78	68	1.71E+00	1001	2.76E+00	3.14E+00
0.2	61	65	1.57E+00	1001	3.10E+00	2.94E+00
0.2	83	74	1.76E+00	1001	2.71E+00	3.22E+00
0.2	64	69	1.62E+00	1001	3.00E+00	3.00E+00
0.3	76	68	1.51E+00	1001	2.49E+00	3.29E+00
0.3	72	65	1.49E+00	1001	2.56E+00	3.23E+00
0.3	67	72	1.45E+00	1001	2.58E+00	2.95E+00
0.3	63	64	1.44E+00	1001	2.57E+00	2.94E+00
0.3	56	64	1.41E+00	1001	2.66E+00	2.81E+00
0.3	79	65	1.52E+00	1001	2.46E+00	3.44E+00
0.3	86	75	1.55E+00	1001	2.39E+00	3.51E+00
0.3	87	72	1.56E+00	1001	2.39E+00	3.62E+00
0.3	64	67	1.45E+00	1001	2.59E+00	3.09E+00
0.3	56	64	1.42E+00	1001	2.63E+00	2.81E+00
0.3	69	63	1.47E+00	1001	2.55E+00	3.11E+00
0.3	45	68	1.35E+00	1001	2.61E+00	2.37E+00
0.3	77	67	1.54E+00	1001	2.45E+00	3.44E+00
0.3	48	64	1.36E+00	1001	2.73E+00	2.60E+00
0.3	60	70	1.43E+00	1001	2.71E+00	3.02E+00
0.3	36	68	1.32E+00	1001	2.75E+00	2.31E+00
0.3	73	70	1.49E+00	1001	2.57E+00	3.32E+00
0.3	83	70	1.55E+00	1001	2.39E+00	3.51E+00
0.3	77	65	1.51E+00	1001	2.50E+00	3.43E+00
0.3	78	68	1.52E+00	1001	2.45E+00	3.31E+00
0.4	32	68	1.23E+00	1001	2.45E+00	2.20E+00
0.4	34	66	1.24E+00	1001	2.49E+00	2.27E+00
0.4	47	69	1.28E+00	1001	2.48E+00	2.69E+00
0.4	45	69	1.27E+00	1001	2.42E+00	2.54E+00
0.4	31	68	1.23E+00	1001	2.43E+00	2.18E+00

0.4	68	66	1.35E+00	1001	2.34E+00	3.21E+00
0.4	35	66	1.25E+00	1001	2.44E+00	2.27E+00
0.4	79	67	1.38E+00	1001	2.31E+00	3.73E+00
0.4	82	66	1.38E+00	1001	2.29E+00	3.78E+00
0.4	68	61	1.35E+00	1001	2.33E+00	3.27E+00
0.4	87	66	1.40E+00	1001	2.26E+00	4.04E+00
0.4	22	69	1.21E+00	1001	2.52E+00	2.05E+00
0.4	52	65	1.29E+00	1001	2.47E+00	2.75E+00
0.4	50	65	1.29E+00	1001	2.48E+00	2.76E+00
0.4	74	67	1.35E+00	1001	2.34E+00	3.47E+00
0.4	66	70	1.34E+00	1001	2.37E+00	3.20E+00
0.4	61	69	1.33E+00	1001	2.40E+00	3.07E+00
0.4	66	64	1.34E+00	1001	2.40E+00	3.19E+00
0.4	72	63	1.36E+00	1001	2.34E+00	3.41E+00
0.4	53	66	1.30E+00	1001	2.37E+00	2.70E+00
0.5	31	66	1.18E+00	1001	2.29E+00	2.21E+00
0.5	37	66	1.19E+00	1001	2.33E+00	2.37E+00
0.5	75	64	1.27E+00	1001	2.21E+00	3.73E+00
0.5	35	65	1.19E+00	1001	2.29E+00	2.34E+00
0.5	31	61	1.18E+00	1001	2.29E+00	2.24E+00
0.5	64	59	1.25E+00	1001	2.26E+00	3.26E+00
0.5	43	66	1.20E+00	1001	2.28E+00	2.53E+00
0.5	70	64	1.27E+00	1001	2.24E+00	3.55E+00
0.5	33	63	1.18E+00	1001	2.28E+00	2.25E+00
0.5	53	61	1.22E+00	1001	2.29E+00	2.83E+00
0.5	84	68	1.29E+00	1001	2.23E+00	4.20E+00
0.5	19	69	1.16E+00	1001	2.24E+00	1.93E+00
0.5	30	64	1.18E+00	1001	2.26E+00	2.17E+00
0.5	34	63	1.18E+00	1001	2.28E+00	2.28E+00
0.5	24	68	1.16E+00	1001	2.27E+00	2.06E+00
0.5	41	62	1.20E+00	1001	2.30E+00	2.48E+00
0.5	38	65	1.19E+00	1001	2.29E+00	2.39E+00
0.5	62	65	1.24E+00	1001	2.25E+00	3.16E+00
0.5	19	67	1.15E+00	1001	2.31E+00	1.96E+00
0.5	46	60	1.21E+00	1001	2.30E+00	2.64E+00
0.6	20	67	1.12E+00	1001	2.13E+00	1.97E+00
0.6	20	67	1.12E+00	1001	2.11E+00	1.94E+00
0.6	79	64	1.21E+00	1001	2.19E+00	4.20E+00
0.6	20	69	1.12E+00	1001	2.14E+00	1.98E+00
0.6	15	68	1.11E+00	1001	2.15E+00	1.86E+00
0.6	23	65	1.13E+00	1001	2.15E+00	2.02E+00
0.6	35	64	1.14E+00	1001	2.20E+00	2.36E+00
0.6	24	70	1.13E+00	1001	2.15E+00	2.04E+00
0.6	29	64	1.13E+00	1001	2.17E+00	2.18E+00
0.6	16	73	1.11E+00	1001	2.13E+00	1.88E+00
0.6	13	70	1.11E+00	1001	2.13E+00	1.84E+00
0.6	37	62	1.14E+00	1001	2.17E+00	2.37E+00
0.6	38	63	1.14E+00	1001	2.20E+00	2.41E+00
0.6	39	63	1.15E+00	1001	2.19E+00	2.49E+00
0.6	29	64	1.13E+00	1001	2.17E+00	2.20E+00
0.6	18	69	1.11E+00	1001	2.13E+00	1.92E+00
0.6	16	69	1.11E+00	1001	2.12E+00	1.88E+00
0.6	30	66	1.13E+00	1001	2.17E+00	2.21E+00
0.6	19	72	1.12E+00	1001	2.14E+00	1.95E+00
0.6	29	62	1.13E+00	1001	2.19E+00	2.20E+00
0.7	24	63	1.09E+00	1001	2.07E+00	2.05E+00
0.7	22	63	1.10E+00	1001	2.05E+00	2.00E+00
0.7	17	67	1.09E+00	1001	2.03E+00	1.90E+00

0.7	17	63	1.09E+00	1001	2.03E+00	1.89E+00
0.7	22	65	1.09E+00	1001	2.07E+00	2.01E+00
0.7	18	66	1.09E+00	1001	2.03E+00	1.92E+00
0.7	21	67	1.09E+00	1001	2.01E+00	1.96E+00
0.7	21	66	1.09E+00	1001	2.07E+00	2.00E+00
0.7	20	65	1.09E+00	1001	2.04E+00	1.96E+00
0.7	20	66	1.09E+00	1001	2.06E+00	1.96E+00
0.7	15	66	1.09E+00	1001	2.03E+00	1.87E+00
0.7	21	63	1.09E+00	1001	2.08E+00	1.99E+00
0.7	20	66	1.10E+00	1001	2.03E+00	1.94E+00
0.7	12	69	1.09E+00	1001	2.00E+00	1.80E+00
0.7	23	67	1.10E+00	1001	2.06E+00	2.03E+00
0.7	21	65	1.10E+00	1001	2.01E+00	1.98E+00
0.7	12	67	1.09E+00	1001	2.01E+00	1.79E+00
0.7	22	64	1.09E+00	1001	2.06E+00	2.02E+00
0.7	21	64	1.09E+00	1001	2.04E+00	1.96E+00
0.7	24	63	1.10E+00	1001	2.05E+00	2.06E+00
0.8	14	66	1.08E+00	1001	1.93E+00	1.82E+00
0.8	19	68	1.08E+00	1001	1.98E+00	1.93E+00
0.8	12	67	1.07E+00	1001	1.96E+00	1.79E+00
0.8	20	66	1.08E+00	1001	1.98E+00	1.96E+00
0.8	17	67	1.07E+00	1001	1.97E+00	1.88E+00
0.8	12	65	1.07E+00	1001	1.95E+00	1.78E+00
0.8	12	67	1.07E+00	1001	1.92E+00	1.78E+00
0.8	21	64	1.08E+00	1001	1.99E+00	1.98E+00
0.8	18	65	1.08E+00	1001	1.95E+00	1.89E+00
0.8	29	60	1.09E+00	1001	2.00E+00	2.17E+00
0.8	19	65	1.08E+00	1001	1.95E+00	1.92E+00
0.8	11	66	1.07E+00	1001	1.94E+00	1.75E+00
0.8	18	66	1.08E+00	1001	1.95E+00	1.89E+00
0.8	14	69	1.07E+00	1001	1.95E+00	1.83E+00
0.8	19	63	1.08E+00	1001	1.97E+00	1.94E+00
0.8	29	67	1.09E+00	1001	1.99E+00	2.19E+00
0.8	14	66	1.08E+00	1001	1.92E+00	1.81E+00
0.8	11	67	1.07E+00	1001	1.93E+00	1.76E+00
0.8	20	63	1.08E+00	1001	1.98E+00	1.96E+00
0.8	17	63	1.08E+00	1001	1.95E+00	1.87E+00
0.9	10	67	1.07E+00	1001	1.88E+00	1.73E+00
0.9	11	65	1.07E+00	1001	1.86E+00	1.71E+00
0.9	13	68	1.07E+00	1001	1.90E+00	1.78E+00
0.9	10	65	1.07E+00	1001	1.87E+00	1.71E+00
0.9	16	65	1.07E+00	1001	1.92E+00	1.84E+00
0.9	12	62	1.07E+00	1001	1.90E+00	1.78E+00
0.9	13	66	1.07E+00	1001	1.90E+00	1.79E+00
0.9	10	69	1.07E+00	1001	1.86E+00	1.70E+00
0.9	14	69	1.07E+00	1001	1.91E+00	1.79E+00
0.9	11	64	1.07E+00	1001	1.88E+00	1.74E+00
0.9	10	66	1.07E+00	1001	1.89E+00	1.72E+00
0.9	15	63	1.07E+00	1001	1.91E+00	1.82E+00
0.9	14	63	1.07E+00	1001	1.89E+00	1.80E+00
0.9	12	64	1.07E+00	1001	1.89E+00	1.76E+00
0.9	14	69	1.07E+00	1001	1.88E+00	1.78E+00
0.9	11	68	1.07E+00	1001	1.87E+00	1.72E+00
0.9	12	68	1.06E+00	1001	1.89E+00	1.75E+00
0.9	12	67	1.07E+00	1001	1.88E+00	1.74E+00
0.9	17	64	1.07E+00	1001	1.92E+00	1.87E+00
0.9	13	65	1.07E+00	1001	1.88E+00	1.77E+00
1.0	13	67	1.08E+00	1001	1.86E+00	1.74E+00

1.0	13	66	1.08E+00	1001	1.87E+00	1.76E+00
1.0	11	65	1.08E+00	1001	1.86E+00	1.72E+00
1.0	12	67	1.08E+00	1001	1.84E+00	1.71E+00
1.0	14	65	1.08E+00	1001	1.88E+00	1.77E+00
1.0	11	66	1.08E+00	1001	1.87E+00	1.73E+00
1.0	11	68	1.08E+00	1001	1.84E+00	1.69E+00
1.0	13	66	1.08E+00	1001	1.87E+00	1.76E+00
1.0	11	65	1.08E+00	1001	1.85E+00	1.70E+00
1.0	7	68	1.07E+00	1001	1.84E+00	1.65E+00
1.0	10	69	1.07E+00	1001	1.86E+00	1.70E+00
1.0	15	66	1.08E+00	1001	1.86E+00	1.77E+00
1.0	21	64	1.08E+00	1001	1.90E+00	1.92E+00
1.0	11	67	1.07E+00	1001	1.84E+00	1.69E+00
1.0	15	69	1.08E+00	1001	1.87E+00	1.76E+00
1.0	16	67	1.08E+00	1001	1.89E+00	1.80E+00
1.0	11	68	1.08E+00	1001	1.85E+00	1.71E+00
1.0	8	70	1.07E+00	1001	1.83E+00	1.65E+00
1.0	12	67	1.08E+00	1001	1.86E+00	1.72E+00
1.0	11	65	1.08E+00	1001	1.84E+00	1.68E+00

Experiment 5.8.2

Movement probability	Average cooperation	Average relatedness	Average interaction length	Model time	Average cell population	Average number of partners
0.0	4	69	1.00E+00	1001	9.28E+01	3.34E+00
0.0	41	69	1.02E+00	1001	8.79E+01	4.54E+00
0.0	33	74	1.01E+00	1001	9.66E+01	4.22E+00
0.0	6	64	1.00E+00	1001	1.11E+02	3.38E+00
0.0	16	66	1.01E+00	1001	1.05E+02	3.67E+00
0.0	44	67	1.01E+00	1001	9.49E+01	4.77E+00
0.0	24	69	1.01E+00	1001	1.10E+02	3.93E+00
0.0	26	65	1.01E+00	1001	1.09E+02	4.04E+00
0.0	3	73	1.01E+00	1001	5.80E+01	3.28E+00
0.0	18	65	1.00E+00	1001	1.05E+02	3.78E+00
0.0	4	68	1.01E+00	1001	7.21E+01	3.30E+00
0.0	31	69	1.01E+00	1001	1.09E+02	4.20E+00
0.0	21	70	1.00E+00	1001	1.16E+02	3.87E+00
0.0	8	67	1.00E+00	1001	1.06E+02	3.43E+00
0.0	24	65	1.01E+00	1001	1.02E+02	3.92E+00
0.0	21	65	1.01E+00	1001	1.06E+02	3.86E+00
0.0	28	71	1.01E+00	1001	1.05E+02	4.09E+00
0.0	14	71	1.00E+00	1001	9.98E+01	3.60E+00
0.0	25	69	1.01E+00	1001	9.24E+01	3.97E+00
0.0	15	70	1.01E+00	1001	9.64E+01	3.64E+00
0.1	9	72	1.07E+00	1001	1.62E+01	3.11E+00
0.1	7	73	1.07E+00	1001	1.58E+01	3.06E+00
0.1	7	71	1.08E+00	1001	1.57E+01	3.07E+00
0.1	12	72	1.09E+00	1001	1.60E+01	3.17E+00
0.1	10	72	1.08E+00	1001	1.59E+01	3.11E+00
0.1	7	71	1.08E+00	1001	1.55E+01	3.05E+00
0.1	8	74	1.08E+00	1001	1.57E+01	3.08E+00
0.1	11	71	1.09E+00	1001	1.57E+01	3.12E+00
0.1	8	71	1.08E+00	1001	1.58E+01	3.06E+00
0.1	8	69	1.08E+00	1001	1.57E+01	3.06E+00
0.1	12	71	1.09E+00	1001	1.58E+01	3.13E+00
0.1	7	72	1.08E+00	1001	1.56E+01	3.04E+00
0.1	7	71	1.08E+00	1001	1.56E+01	3.04E+00
0.1	8	69	1.08E+00	1001	1.56E+01	3.06E+00
0.1	11	69	1.08E+00	1001	1.60E+01	3.14E+00

0.1	7	70	1.07E+00	1001	1.59E+01	3.05E+00
0.1	7	71	1.07E+00	1001	1.56E+01	3.05E+00
0.1	11	73	1.09E+00	1001	1.59E+01	3.13E+00
0.1	10	71	1.08E+00	1001	1.60E+01	3.13E+00
0.1	10	71	1.08E+00	1001	1.58E+01	3.13E+00
0.2	6	70	1.11E+00	1001	1.54E+01	2.93E+00
0.2	9	68	1.11E+00	1001	1.56E+01	3.00E+00
0.2	8	71	1.11E+00	1001	1.55E+01	2.97E+00
0.2	7	69	1.11E+00	1001	1.55E+01	2.94E+00
0.2	6	73	1.11E+00	1001	1.55E+01	2.93E+00
0.2	7	70	1.11E+00	1001	1.54E+01	2.93E+00
0.2	8	71	1.11E+00	1001	1.55E+01	2.96E+00
0.2	7	69	1.11E+00	1001	1.55E+01	2.95E+00
0.2	7	71	1.11E+00	1001	1.55E+01	2.95E+00
0.2	6	71	1.11E+00	1001	1.55E+01	2.95E+00
0.2	8	70	1.12E+00	1001	1.56E+01	2.98E+00
0.2	7	66	1.11E+00	1001	1.55E+01	2.96E+00
0.2	6	70	1.11E+00	1001	1.54E+01	2.94E+00
0.2	6	70	1.11E+00	1001	1.54E+01	2.92E+00
0.2	6	70	1.11E+00	1001	1.54E+01	2.92E+00
0.2	8	71	1.12E+00	1001	1.55E+01	2.97E+00
0.2	9	70	1.12E+00	1001	1.55E+01	3.00E+00
0.2	8	72	1.11E+00	1001	1.55E+01	2.98E+00
0.2	9	69	1.12E+00	1001	1.55E+01	2.97E+00
0.2	8	69	1.11E+00	1001	1.55E+01	2.98E+00
0.3	7	69	1.12E+00	1001	1.55E+01	2.95E+00
0.3	7	68	1.12E+00	1001	1.55E+01	2.94E+00
0.3	7	69	1.12E+00	1001	1.54E+01	2.93E+00
0.3	6	69	1.12E+00	1001	1.54E+01	2.92E+00
0.3	6	69	1.11E+00	1001	1.54E+01	2.90E+00
0.3	5	70	1.11E+00	1001	1.54E+01	2.90E+00
0.3	7	69	1.12E+00	1001	1.55E+01	2.95E+00
0.3	8	66	1.12E+00	1001	1.55E+01	2.96E+00
0.3	7	69	1.12E+00	1001	1.55E+01	2.94E+00
0.3	7	70	1.12E+00	1001	1.54E+01	2.93E+00
0.3	6	69	1.11E+00	1001	1.54E+01	2.90E+00
0.3	8	67	1.12E+00	1001	1.55E+01	2.95E+00
0.3	7	69	1.12E+00	1001	1.54E+01	2.94E+00
0.3	6	70	1.12E+00	1001	1.54E+01	2.89E+00
0.3	5	70	1.11E+00	1001	1.53E+01	2.90E+00
0.3	6	69	1.12E+00	1001	1.54E+01	2.92E+00
0.3	5	68	1.11E+00	1001	1.54E+01	2.91E+00
0.3	7	68	1.12E+00	1001	1.55E+01	2.94E+00
0.3	7	70	1.11E+00	1001	1.55E+01	2.95E+00
0.3	6	69	1.12E+00	1001	1.54E+01	2.93E+00
0.4	5	68	1.10E+00	1001	1.54E+01	2.92E+00
0.4	4	69	1.10E+00	1001	1.53E+01	2.90E+00
0.4	5	70	1.10E+00	1001	1.53E+01	2.91E+00
0.4	6	71	1.10E+00	1001	1.54E+01	2.93E+00
0.4	5	67	1.10E+00	1001	1.54E+01	2.95E+00
0.4	5	66	1.10E+00	1001	1.54E+01	2.93E+00
0.4	5	71	1.10E+00	1001	1.54E+01	2.92E+00
0.4	6	69	1.10E+00	1001	1.54E+01	2.94E+00
0.4	6	68	1.10E+00	1001	1.54E+01	2.93E+00
0.4	6	67	1.10E+00	1001	1.54E+01	2.96E+00
0.4	6	69	1.10E+00	1001	1.54E+01	2.95E+00
0.4	4	70	1.10E+00	1001	1.53E+01	2.91E+00
0.4	4	69	1.10E+00	1001	1.53E+01	2.90E+00

0.4	6	65	1.10E+00	1001	1.54E+01	2.94E+00
0.4	6	68	1.10E+00	1001	1.54E+01	2.95E+00
0.4	4	69	1.10E+00	1001	1.54E+01	2.92E+00
0.4	4	71	1.10E+00	1001	1.54E+01	2.89E+00
0.4	6	67	1.10E+00	1001	1.54E+01	2.93E+00
0.4	4	70	1.10E+00	1001	1.53E+01	2.90E+00
0.4	6	67	1.10E+00	1001	1.53E+01	2.93E+00
0.5	6	68	1.08E+00	1001	1.54E+01	2.98E+00
0.5	3	71	1.08E+00	1001	1.53E+01	2.93E+00
0.5	5	65	1.08E+00	1001	1.54E+01	2.96E+00
0.5	4	69	1.08E+00	1001	1.54E+01	2.94E+00
0.5	4	69	1.08E+00	1001	1.53E+01	2.94E+00
0.5	4	69	1.08E+00	1001	1.53E+01	2.95E+00
0.5	4	69	1.08E+00	1001	1.53E+01	2.93E+00
0.5	5	66	1.08E+00	1001	1.54E+01	2.96E+00
0.5	5	66	1.08E+00	1001	1.54E+01	2.97E+00
0.5	3	67	1.08E+00	1001	1.53E+01	2.90E+00
0.5	5	66	1.08E+00	1001	1.54E+01	2.97E+00
0.5	5	69	1.08E+00	1001	1.54E+01	2.96E+00
0.5	4	68	1.08E+00	1001	1.53E+01	2.93E+00
0.5	4	70	1.08E+00	1001	1.53E+01	2.94E+00
0.5	3	69	1.08E+00	1001	1.53E+01	2.93E+00
0.5	4	68	1.08E+00	1001	1.53E+01	2.96E+00
0.5	4	68	1.09E+00	1001	1.53E+01	2.92E+00
0.5	3	71	1.08E+00	1001	1.53E+01	2.93E+00
0.5	5	66	1.09E+00	1001	1.54E+01	2.96E+00
0.5	4	66	1.08E+00	1001	1.53E+01	2.94E+00
0.6	4	67	1.07E+00	1001	1.53E+01	2.95E+00
0.6	4	69	1.07E+00	1001	1.53E+01	2.97E+00
0.6	4	71	1.07E+00	1001	1.53E+01	2.95E+00
0.6	4	71	1.07E+00	1001	1.53E+01	2.95E+00
0.6	4	66	1.08E+00	1001	1.53E+01	2.95E+00
0.6	4	67	1.07E+00	1001	1.53E+01	2.98E+00
0.6	3	69	1.07E+00	1001	1.52E+01	2.92E+00
0.6	4	69	1.07E+00	1001	1.53E+01	2.96E+00
0.6	4	66	1.07E+00	1001	1.53E+01	2.96E+00
0.6	4	69	1.07E+00	1001	1.53E+01	2.97E+00
0.6	4	69	1.07E+00	1001	1.53E+01	2.95E+00
0.6	3	70	1.07E+00	1001	1.53E+01	2.94E+00
0.6	5	67	1.07E+00	1001	1.53E+01	2.97E+00
0.6	5	67	1.08E+00	1001	1.54E+01	2.99E+00
0.6	4	67	1.07E+00	1001	1.53E+01	2.97E+00
0.6	5	65	1.08E+00	1001	1.54E+01	3.01E+00
0.6	4	72	1.08E+00	1001	1.53E+01	2.95E+00
0.6	4	66	1.07E+00	1001	1.53E+01	2.98E+00
0.6	4	69	1.07E+00	1001	1.53E+01	2.95E+00
0.6	3	67	1.07E+00	1001	1.53E+01	2.93E+00
0.7	3	70	1.07E+00	1001	1.53E+01	2.92E+00
0.7	4	68	1.07E+00	1001	1.53E+01	2.94E+00
0.7	3	65	1.07E+00	1001	1.53E+01	2.95E+00
0.7	3	68	1.07E+00	1001	1.53E+01	2.94E+00
0.7	3	71	1.07E+00	1001	1.53E+01	2.94E+00
0.7	4	67	1.07E+00	1001	1.53E+01	2.95E+00
0.7	3	67	1.07E+00	1001	1.53E+01	2.94E+00
0.7	3	69	1.07E+00	1001	1.53E+01	2.94E+00
0.7	3	68	1.07E+00	1001	1.53E+01	2.92E+00
0.7	3	68	1.07E+00	1001	1.53E+01	2.95E+00
0.7	3	68	1.07E+00	1001	1.53E+01	2.92E+00

0.7	3	70	1.07E+00	1001	1.53E+01	2.94E+00
0.7	3	70	1.07E+00	1001	1.53E+01	2.92E+00
0.7	3	68	1.07E+00	1001	1.53E+01	2.94E+00
0.7	3	67	1.07E+00	1001	1.53E+01	2.93E+00
0.7	3	67	1.07E+00	1001	1.52E+01	2.92E+00
0.7	4	71	1.07E+00	1001	1.53E+01	2.94E+00
0.7	4	70	1.07E+00	1001	1.53E+01	2.95E+00
0.7	3	66	1.07E+00	1001	1.53E+01	2.94E+00
0.7	3	71	1.07E+00	1001	1.53E+01	2.92E+00
0.8	3	68	1.09E+00	1001	1.53E+01	2.89E+00
0.8	4	67	1.09E+00	1001	1.53E+01	2.89E+00
0.8	3	71	1.09E+00	1001	1.53E+01	2.90E+00
0.8	4	69	1.09E+00	1001	1.53E+01	2.91E+00
0.8	3	70	1.09E+00	1001	1.53E+01	2.88E+00
0.8	3	71	1.09E+00	1001	1.53E+01	2.90E+00
0.8	4	68	1.09E+00	1001	1.53E+01	2.91E+00
0.8	4	66	1.09E+00	1001	1.53E+01	2.90E+00
0.8	3	71	1.09E+00	1001	1.52E+01	2.88E+00
0.8	3	70	1.09E+00	1001	1.52E+01	2.87E+00
0.8	4	67	1.09E+00	1001	1.53E+01	2.90E+00
0.8	4	67	1.09E+00	1001	1.53E+01	2.91E+00
0.8	3	71	1.09E+00	1001	1.52E+01	2.87E+00
0.8	4	68	1.09E+00	1001	1.53E+01	2.92E+00
0.8	4	69	1.09E+00	1001	1.53E+01	2.91E+00
0.8	3	72	1.09E+00	1001	1.52E+01	2.88E+00
0.8	2	70	1.09E+00	1001	1.52E+01	2.86E+00
0.8	3	67	1.09E+00	1001	1.53E+01	2.90E+00
0.8	4	66	1.09E+00	1001	1.53E+01	2.91E+00
0.8	3	68	1.09E+00	1001	1.53E+01	2.88E+00
0.9	3	70	1.13E+00	1001	1.53E+01	2.78E+00
0.9	3	69	1.13E+00	1001	1.53E+01	2.79E+00
0.9	4	68	1.13E+00	1001	1.52E+01	2.80E+00
0.9	4	68	1.12E+00	1001	1.53E+01	2.80E+00
0.9	3	69	1.12E+00	1001	1.53E+01	2.80E+00
0.9	3	68	1.13E+00	1001	1.53E+01	2.79E+00
0.9	3	68	1.13E+00	1001	1.53E+01	2.79E+00
0.9	4	71	1.13E+00	1001	1.53E+01	2.81E+00
0.9	3	70	1.12E+00	1001	1.53E+01	2.79E+00
0.9	2	70	1.12E+00	1001	1.52E+01	2.78E+00
0.9	3	67	1.12E+00	1001	1.53E+01	2.80E+00
0.9	3	68	1.12E+00	1001	1.53E+01	2.80E+00
0.9	4	67	1.13E+00	1001	1.53E+01	2.82E+00
0.9	2	69	1.12E+00	1001	1.52E+01	2.79E+00
0.9	3	68	1.13E+00	1001	1.53E+01	2.78E+00
0.9	3	70	1.13E+00	1001	1.53E+01	2.78E+00
0.9	3	70	1.13E+00	1001	1.53E+01	2.79E+00
0.9	2	70	1.12E+00	1001	1.52E+01	2.77E+00
0.9	3	69	1.12E+00	1001	1.53E+01	2.78E+00
0.9	3	69	1.12E+00	1001	1.53E+01	2.80E+00
1.0	2	68	1.19E+00	1001	1.52E+01	2.63E+00
1.0	3	72	1.19E+00	1001	1.52E+01	2.63E+00
1.0	3	70	1.19E+00	1001	1.53E+01	2.64E+00
1.0	2	73	1.19E+00	1001	1.52E+01	2.63E+00
1.0	3	70	1.19E+00	1001	1.53E+01	2.62E+00
1.0	3	70	1.19E+00	1001	1.53E+01	2.63E+00
1.0	2	70	1.19E+00	1001	1.52E+01	2.61E+00
1.0	2	71	1.19E+00	1001	1.52E+01	2.62E+00
1.0	3	70	1.19E+00	1001	1.53E+01	2.66E+00

1.0	3	71	1.19E+00	1001	1.53E+01	2.63E+00
1.0	3	71	1.19E+00	1001	1.53E+01	2.65E+00
1.0	3	72	1.19E+00	1001	1.53E+01	2.64E+00
1.0	3	68	1.19E+00	1001	1.52E+01	2.64E+00
1.0	3	72	1.19E+00	1001	1.52E+01	2.63E+00
1.0	3	72	1.19E+00	1001	1.53E+01	2.63E+00
1.0	3	68	1.19E+00	1001	1.52E+01	2.63E+00
1.0	2	69	1.19E+00	1001	1.52E+01	2.62E+00
1.0	3	73	1.19E+00	1001	1.53E+01	2.64E+00
1.0	3	68	1.19E+00	1001	1.53E+01	2.64E+00
1.0	2	72	1.19E+00	1001	1.52E+01	2.62E+00

Experiment 5.9.2

Movement probability	Average cooperation	Average relatedness	Average interaction length	Model time	Average cell population	Average number of partners
0.0	45	73	3.05E+00	1001	7.47E+01	5.29E+00
0.0	50	71	3.05E+00	1001	7.54E+01	5.28E+00
0.0	55	74	3.04E+00	1001	7.69E+01	5.68E+00
0.0	48	72	3.11E+00	1001	6.12E+01	4.97E+00
0.0	82	75	3.07E+00	1001	6.89E+01	8.18E+00
0.0	76	77	3.11E+00	1001	5.75E+01	7.32E+00
0.0	27	74	3.08E+00	1001	5.92E+01	4.12E+00
0.0	56	74	3.05E+00	1001	8.00E+01	5.63E+00
0.0	45	69	3.05E+00	1001	7.61E+01	5.10E+00
0.0	47	72	3.06E+00	1001	7.16E+01	5.35E+00
0.0	57	73	3.08E+00	1001	6.33E+01	5.69E+00
0.0	44	73	3.05E+00	1001	7.30E+01	4.99E+00
0.0	66	74	3.10E+00	1001	6.00E+01	6.39E+00
0.0	69	71	3.06E+00	1001	7.32E+01	7.02E+00
0.0	45	70	3.09E+00	1001	6.35E+01	4.94E+00
0.0	44	72	3.05E+00	1001	6.76E+01	5.00E+00
0.0	32	70	3.03E+00	1001	8.09E+01	4.44E+00
0.0	49	67	3.05E+00	1001	7.63E+01	5.49E+00
0.0	78	78	3.07E+00	1001	6.91E+01	7.64E+00
0.0	71	74	3.10E+00	1001	6.32E+01	7.07E+00
0.1	81	76	5.17E+00	1001	4.40E+00	3.17E+00
0.1	81	77	5.16E+00	1001	4.35E+00	3.13E+00
0.1	87	77	5.26E+00	1001	4.33E+00	3.19E+00
0.1	69	73	4.76E+00	1001	4.61E+00	3.13E+00
0.1	86	75	5.21E+00	1001	4.52E+00	3.28E+00
0.1	46	75	4.18E+00	1001	4.63E+00	2.83E+00
0.1	65	72	4.66E+00	1001	4.71E+00	3.10E+00
0.1	83	76	5.11E+00	1001	4.38E+00	3.15E+00
0.1	79	73	5.11E+00	1001	4.22E+00	3.04E+00
0.1	80	76	5.16E+00	1001	4.38E+00	3.15E+00
0.1	80	75	5.06E+00	1001	4.39E+00	3.10E+00
0.1	64	75	4.64E+00	1001	4.50E+00	2.98E+00
0.1	86	77	5.26E+00	1001	4.50E+00	3.25E+00
0.1	56	74	4.52E+00	1001	4.72E+00	2.96E+00
0.1	82	77	5.16E+00	1001	4.42E+00	3.17E+00
0.1	86	77	5.23E+00	1001	4.48E+00	3.24E+00
0.1	62	74	4.67E+00	1001	4.54E+00	3.02E+00
0.1	82	75	5.07E+00	1001	4.52E+00	3.26E+00
0.1	78	77	5.01E+00	1001	4.50E+00	3.18E+00
0.1	84	76	5.21E+00	1001	4.53E+00	3.25E+00
0.2	69	73	4.52E+00	1001	3.37E+00	2.85E+00
0.2	72	72	4.57E+00	1001	3.44E+00	2.90E+00
0.2	68	72	4.48E+00	1001	3.36E+00	2.81E+00

0.2	74	71	4.61E+00	1001	3.40E+00	2.97E+00
0.2	42	73	4.14E+00	1001	3.42E+00	2.47E+00
0.2	85	77	4.79E+00	1001	3.39E+00	3.15E+00
0.2	49	73	4.25E+00	1001	3.37E+00	2.54E+00
0.2	41	75	4.13E+00	1001	3.41E+00	2.46E+00
0.2	86	79	4.78E+00	1001	3.37E+00	3.07E+00
0.2	77	75	4.66E+00	1001	3.35E+00	2.94E+00
0.2	85	78	4.78E+00	1001	3.29E+00	3.03E+00
0.2	83	78	4.73E+00	1001	3.44E+00	3.10E+00
0.2	78	76	4.70E+00	1001	3.34E+00	2.97E+00
0.2	66	73	4.48E+00	1001	3.40E+00	2.80E+00
0.2	77	74	4.65E+00	1001	3.40E+00	2.97E+00
0.2	79	75	4.72E+00	1001	3.31E+00	2.99E+00
0.2	68	73	4.49E+00	1001	3.38E+00	2.84E+00
0.2	58	73	4.36E+00	1001	3.49E+00	2.73E+00
0.2	86	78	4.80E+00	1001	3.35E+00	3.10E+00
0.2	34	72	3.99E+00	1001	3.57E+00	2.42E+00
0.3	79	71	4.28E+00	1001	2.81E+00	2.97E+00
0.3	71	75	4.20E+00	1001	2.84E+00	2.82E+00
0.3	22	71	3.79E+00	1001	2.87E+00	2.16E+00
0.3	78	76	4.26E+00	1001	2.84E+00	2.96E+00
0.3	27	73	3.84E+00	1001	2.90E+00	2.26E+00
0.3	55	75	4.07E+00	1001	2.90E+00	2.58E+00
0.3	84	76	4.32E+00	1001	2.80E+00	3.01E+00
0.3	51	67	4.05E+00	1001	2.88E+00	2.61E+00
0.3	40	73	3.93E+00	1001	2.91E+00	2.38E+00
0.3	77	77	4.25E+00	1001	2.83E+00	2.91E+00
0.3	29	66	3.85E+00	1001	2.93E+00	2.27E+00
0.3	81	75	4.28E+00	1001	2.84E+00	3.02E+00
0.3	82	78	4.29E+00	1001	2.89E+00	3.08E+00
0.3	74	75	4.24E+00	1001	2.72E+00	2.81E+00
0.3	75	74	4.22E+00	1001	2.91E+00	2.93E+00
0.3	59	74	4.09E+00	1001	2.91E+00	2.65E+00
0.3	67	71	4.18E+00	1001	2.88E+00	2.87E+00
0.3	78	75	4.26E+00	1001	2.83E+00	2.94E+00
0.3	61	71	4.13E+00	1001	2.88E+00	2.81E+00
0.3	82	77	4.29E+00	1001	2.86E+00	3.06E+00
0.4	59	72	3.83E+00	1001	2.55E+00	2.65E+00
0.4	27	72	3.65E+00	1001	2.60E+00	2.23E+00
0.4	37	71	3.72E+00	1001	2.57E+00	2.33E+00
0.4	57	72	3.80E+00	1001	2.62E+00	2.65E+00
0.4	78	75	3.94E+00	1001	2.56E+00	3.03E+00
0.4	33	73	3.69E+00	1001	2.61E+00	2.30E+00
0.4	73	73	3.91E+00	1001	2.53E+00	2.89E+00
0.4	78	72	3.94E+00	1001	2.55E+00	3.02E+00
0.4	16	73	3.59E+00	1001	2.59E+00	2.08E+00
0.4	59	72	3.85E+00	1001	2.53E+00	2.63E+00
0.4	18	71	3.61E+00	1001	2.61E+00	2.12E+00
0.4	48	71	3.78E+00	1001	2.58E+00	2.56E+00
0.4	54	68	3.78E+00	1001	2.59E+00	2.61E+00
0.4	22	70	3.64E+00	1001	2.59E+00	2.19E+00
0.4	74	76	3.91E+00	1001	2.54E+00	2.89E+00
0.4	19	71	3.62E+00	1001	2.59E+00	2.13E+00
0.4	76	74	3.95E+00	1001	2.48E+00	2.90E+00
0.4	73	79	3.91E+00	1001	2.54E+00	2.91E+00
0.4	55	70	3.82E+00	1001	2.54E+00	2.61E+00
0.4	21	71	3.63E+00	1001	2.57E+00	2.13E+00
0.5	49	70	3.59E+00	1001	2.30E+00	2.47E+00

0.5	43	72	3.58E+00	1001	2.31E+00	2.40E+00
0.5	22	67	3.51E+00	1001	2.29E+00	2.11E+00
0.5	24	73	3.49E+00	1001	2.37E+00	2.20E+00
0.5	62	77	3.64E+00	1001	2.35E+00	2.71E+00
0.5	21	72	3.49E+00	1001	2.38E+00	2.14E+00
0.5	42	70	3.59E+00	1001	2.33E+00	2.44E+00
0.5	23	70	3.50E+00	1001	2.34E+00	2.16E+00
0.5	18	70	3.48E+00	1001	2.33E+00	2.09E+00
0.5	68	76	3.65E+00	1001	2.33E+00	2.83E+00
0.5	69	76	3.66E+00	1001	2.34E+00	2.85E+00
0.5	15	74	3.47E+00	1001	2.33E+00	2.06E+00
0.5	26	72	3.52E+00	1001	2.35E+00	2.18E+00
0.5	49	71	3.61E+00	1001	2.35E+00	2.48E+00
0.5	65	75	3.66E+00	1001	2.38E+00	2.78E+00
0.5	82	80	3.71E+00	1001	2.40E+00	3.14E+00
0.5	53	72	3.62E+00	1001	2.38E+00	2.60E+00
0.5	21	68	3.49E+00	1001	2.36E+00	2.13E+00
0.5	56	80	3.62E+00	1001	2.39E+00	2.63E+00
0.5	25	71	3.50E+00	1001	2.36E+00	2.20E+00
0.6	68	73	3.50E+00	1001	2.22E+00	2.92E+00
0.6	17	69	3.37E+00	1001	2.18E+00	2.05E+00
0.6	13	74	3.36E+00	1001	2.16E+00	1.99E+00
0.6	23	71	3.39E+00	1001	2.22E+00	2.15E+00
0.6	62	73	3.48E+00	1001	2.24E+00	2.77E+00
0.6	21	71	3.38E+00	1001	2.18E+00	2.12E+00
0.6	29	66	3.41E+00	1001	2.19E+00	2.25E+00
0.6	72	71	3.51E+00	1001	2.24E+00	2.99E+00
0.6	30	72	3.40E+00	1001	2.20E+00	2.24E+00
0.6	54	72	3.47E+00	1001	2.23E+00	2.62E+00
0.6	23	70	3.39E+00	1001	2.18E+00	2.14E+00
0.6	36	71	3.42E+00	1001	2.20E+00	2.31E+00
0.6	15	71	3.37E+00	1001	2.16E+00	2.03E+00
0.6	28	68	3.40E+00	1001	2.19E+00	2.21E+00
0.6	13	73	3.36E+00	1001	2.18E+00	1.99E+00
0.6	67	69	3.51E+00	1001	2.21E+00	2.89E+00
0.6	16	72	3.36E+00	1001	2.19E+00	2.07E+00
0.6	37	72	3.43E+00	1001	2.23E+00	2.34E+00
0.6	56	72	3.47E+00	1001	2.24E+00	2.67E+00
0.6	55	75	3.47E+00	1001	2.21E+00	2.61E+00
0.7	39	68	3.33E+00	1001	2.13E+00	2.41E+00
0.7	60	69	3.38E+00	1001	2.15E+00	2.81E+00
0.7	16	70	3.30E+00	1001	2.05E+00	2.01E+00
0.7	58	73	3.37E+00	1001	2.13E+00	2.72E+00
0.7	17	72	3.30E+00	1001	2.09E+00	2.07E+00
0.7	15	68	3.29E+00	1001	2.06E+00	2.01E+00
0.7	53	70	3.36E+00	1001	2.15E+00	2.66E+00
0.7	13	71	3.28E+00	1001	2.09E+00	2.02E+00
0.7	18	70	3.29E+00	1001	2.08E+00	2.08E+00
0.7	18	71	3.30E+00	1001	2.10E+00	2.07E+00
0.7	23	66	3.30E+00	1001	2.06E+00	2.12E+00
0.7	23	67	3.31E+00	1001	2.08E+00	2.14E+00
0.7	53	74	3.37E+00	1001	2.10E+00	2.56E+00
0.7	32	72	3.31E+00	1001	2.12E+00	2.27E+00
0.7	24	68	3.31E+00	1001	2.07E+00	2.13E+00
0.7	64	75	3.38E+00	1001	2.15E+00	2.81E+00
0.7	21	68	3.30E+00	1001	2.08E+00	2.11E+00
0.7	33	73	3.32E+00	1001	2.09E+00	2.26E+00
0.7	53	75	3.36E+00	1001	2.14E+00	2.61E+00

0.7	37	75	3.34E+00	1001	2.10E+00	2.31E+00
0.8	57	69	3.30E+00	1001	2.08E+00	2.72E+00
0.8	28	66	3.26E+00	1001	2.03E+00	2.19E+00
0.8	12	72	3.23E+00	1001	1.99E+00	1.95E+00
0.8	17	72	3.24E+00	1001	2.01E+00	2.04E+00
0.8	16	72	3.24E+00	1001	2.02E+00	2.02E+00
0.8	36	68	3.27E+00	1001	2.05E+00	2.34E+00
0.8	25	64	3.25E+00	1001	2.02E+00	2.19E+00
0.8	13	72	3.24E+00	1001	1.98E+00	1.96E+00
0.8	20	68	3.25E+00	1001	2.00E+00	2.06E+00
0.8	11	72	3.23E+00	1001	1.99E+00	1.95E+00
0.8	24	66	3.25E+00	1001	2.02E+00	2.14E+00
0.8	19	70	3.24E+00	1001	2.03E+00	2.08E+00
0.8	33	65	3.26E+00	1001	2.03E+00	2.30E+00
0.8	17	70	3.25E+00	1001	1.98E+00	2.02E+00
0.8	60	74	3.30E+00	1001	2.08E+00	2.76E+00
0.8	24	66	3.25E+00	1001	2.03E+00	2.16E+00
0.8	30	65	3.26E+00	1001	2.04E+00	2.28E+00
0.8	42	71	3.29E+00	1001	2.06E+00	2.44E+00
0.8	15	72	3.23E+00	1001	2.01E+00	2.02E+00
0.8	17	71	3.25E+00	1001	1.99E+00	2.03E+00
0.9	18	69	3.23E+00	1001	1.96E+00	2.02E+00
0.9	13	69	3.22E+00	1001	1.95E+00	1.94E+00
0.9	19	68	3.23E+00	1001	1.97E+00	2.06E+00
0.9	53	72	3.28E+00	1001	2.04E+00	2.62E+00
0.9	12	72	3.22E+00	1001	1.95E+00	1.95E+00
0.9	10	75	3.22E+00	1001	1.94E+00	1.91E+00
0.9	32	68	3.25E+00	1001	2.00E+00	2.29E+00
0.9	30	70	3.25E+00	1001	1.99E+00	2.22E+00
0.9	29	65	3.24E+00	1001	2.00E+00	2.25E+00
0.9	42	71	3.26E+00	1001	2.01E+00	2.40E+00
0.9	13	72	3.22E+00	1001	1.95E+00	1.95E+00
0.9	35	70	3.25E+00	1001	2.01E+00	2.29E+00
0.9	15	68	3.22E+00	1001	1.95E+00	1.98E+00
0.9	18	69	3.23E+00	1001	1.96E+00	2.04E+00
0.9	14	68	3.22E+00	1001	1.97E+00	1.98E+00
0.9	17	70	3.23E+00	1001	1.96E+00	2.02E+00
0.9	18	70	3.23E+00	1001	1.96E+00	2.03E+00
0.9	20	65	3.24E+00	1001	1.97E+00	2.08E+00
0.9	28	69	3.25E+00	1001	1.98E+00	2.19E+00
0.9	17	69	3.23E+00	1001	1.95E+00	2.01E+00
1.0	13	71	3.25E+00	1001	1.92E+00	1.93E+00
1.0	18	70	3.26E+00	1001	1.93E+00	1.99E+00
1.0	15	70	3.25E+00	1001	1.92E+00	1.96E+00
1.0	35	70	3.27E+00	1001	1.99E+00	2.28E+00
1.0	18	70	3.26E+00	1001	1.94E+00	1.98E+00
1.0	18	70	3.26E+00	1001	1.92E+00	1.99E+00
1.0	18	68	3.26E+00	1001	1.93E+00	1.99E+00
1.0	21	74	3.26E+00	1001	1.92E+00	2.02E+00
1.0	59	74	3.32E+00	1001	2.03E+00	2.71E+00
1.0	37	70	3.27E+00	1001	1.98E+00	2.28E+00
1.0	13	73	3.25E+00	1001	1.93E+00	1.92E+00
1.0	15	71	3.26E+00	1001	1.94E+00	1.98E+00
1.0	19	69	3.26E+00	1001	1.93E+00	2.00E+00
1.0	36	72	3.28E+00	1001	1.98E+00	2.28E+00
1.0	16	70	3.25E+00	1001	1.93E+00	1.96E+00
1.0	20	68	3.26E+00	1001	1.96E+00	2.04E+00
1.0	11	72	3.25E+00	1001	1.92E+00	1.88E+00

1.0	11	73	3.24E+00	1001	1.91E+00	1.88E+00
1.0	19	68	3.26E+00	1001	1.95E+00	2.03E+00
1.0	47	66	3.29E+00	1001	2.01E+00	2.51E+00

Experiment 5.10.2

Movement probability	Average cooperation	Average relatedness	Average interaction length	Model time	Average cell population	Average number of partners
0.0	0	65	1.00E+00	1001	5.78E+01	3.88E+00
0.0	0	66	1.00E+00	1001	4.82E+01	3.85E+00
0.0	0	67	1.00E+00	1001	5.97E+01	3.89E+00
0.0	0	63	1.00E+00	1001	6.25E+01	3.84E+00
0.0	0	68	1.00E+00	1001	4.99E+01	3.84E+00
0.0	0	67	1.00E+00	1001	5.16E+01	3.83E+00
0.0	0	67	1.01E+00	1001	4.81E+01	3.92E+00
0.0	0	67	1.00E+00	1001	5.61E+01	3.88E+00
0.0	0	69	1.01E+00	1001	4.87E+01	3.95E+00
0.0	0	67	1.00E+00	1001	5.96E+01	3.72E+00
0.0	0	65	1.00E+00	1001	5.93E+01	3.95E+00
0.0	0	66	1.00E+00	1001	5.55E+01	3.93E+00
0.0	0	63	1.00E+00	1001	5.25E+01	3.87E+00
0.0	0	64	1.00E+00	1001	5.04E+01	3.83E+00
0.0	0	65	1.00E+00	1001	6.45E+01	4.00E+00
0.0	0	65	1.00E+00	1001	5.22E+01	3.88E+00
0.0	0	66	1.00E+00	1001	5.62E+01	3.90E+00
0.0	0	65	1.01E+00	1001	5.00E+01	3.93E+00
0.0	0	65	1.00E+00	1001	5.44E+01	3.89E+00
0.0	0	69	1.00E+00	1001	5.17E+01	3.84E+00
0.1	8	72	1.25E+00	1001	3.88E+00	2.28E+00
0.1	9	72	1.27E+00	1001	3.93E+00	2.32E+00
0.1	8	76	1.25E+00	1001	3.86E+00	2.25E+00
0.1	8	70	1.24E+00	1001	4.09E+00	2.35E+00
0.1	7	74	1.24E+00	1001	3.97E+00	2.31E+00
0.1	8	72	1.25E+00	1001	4.07E+00	2.36E+00
0.1	8	75	1.25E+00	1001	3.98E+00	2.30E+00
0.1	9	76	1.26E+00	1001	3.86E+00	2.28E+00
0.1	7	71	1.23E+00	1001	4.06E+00	2.29E+00
0.1	8	75	1.25E+00	1001	4.00E+00	2.32E+00
0.1	8	73	1.25E+00	1001	3.92E+00	2.29E+00
0.1	8	74	1.24E+00	1001	4.05E+00	2.29E+00
0.1	8	74	1.24E+00	1001	4.00E+00	2.32E+00
0.1	9	75	1.26E+00	1001	3.94E+00	2.31E+00
0.1	9	72	1.26E+00	1001	4.01E+00	2.33E+00
0.1	7	72	1.24E+00	1001	3.88E+00	2.25E+00
0.1	7	74	1.22E+00	1001	4.10E+00	2.31E+00
0.1	8	74	1.25E+00	1001	4.00E+00	2.30E+00
0.1	7	74	1.24E+00	1001	3.95E+00	2.32E+00
0.1	10	74	1.27E+00	1001	4.00E+00	2.35E+00
0.2	11	75	1.33E+00	1001	2.78E+00	1.98E+00
0.2	10	72	1.30E+00	1001	2.76E+00	1.92E+00
0.2	9	72	1.29E+00	1001	2.88E+00	1.96E+00
0.2	10	73	1.30E+00	1001	2.83E+00	1.93E+00
0.2	9	72	1.30E+00	1001	2.79E+00	1.93E+00
0.2	10	73	1.30E+00	1001	2.81E+00	1.95E+00
0.2	10	69	1.30E+00	1001	2.86E+00	1.95E+00
0.2	10	72	1.30E+00	1001	2.76E+00	1.93E+00
0.2	10	74	1.30E+00	1001	2.84E+00	1.95E+00
0.2	11	75	1.32E+00	1001	2.79E+00	1.97E+00
0.2	10	73	1.31E+00	1001	2.67E+00	1.88E+00

0.2	9	70	1.29E+00	1001	2.80E+00	1.95E+00
0.2	9	71	1.29E+00	1001	2.76E+00	1.89E+00
0.2	10	72	1.31E+00	1001	2.82E+00	1.97E+00
0.2	10	71	1.31E+00	1001	2.89E+00	2.00E+00
0.2	8	73	1.28E+00	1001	2.83E+00	1.92E+00
0.2	9	69	1.29E+00	1001	2.77E+00	1.90E+00
0.2	9	72	1.30E+00	1001	2.82E+00	1.94E+00
0.2	10	72	1.30E+00	1001	2.80E+00	1.98E+00
0.2	11	73	1.31E+00	1001	2.78E+00	1.93E+00
0.3	8	73	1.26E+00	1001	2.34E+00	1.77E+00
0.3	9	71	1.27E+00	1001	2.31E+00	1.82E+00
0.3	8	71	1.26E+00	1001	2.35E+00	1.78E+00
0.3	10	71	1.27E+00	1001	2.35E+00	1.81E+00
0.3	9	73	1.28E+00	1001	2.35E+00	1.82E+00
0.3	10	74	1.27E+00	1001	2.37E+00	1.82E+00
0.3	9	72	1.27E+00	1001	2.29E+00	1.75E+00
0.3	10	70	1.27E+00	1001	2.37E+00	1.86E+00
0.3	10	75	1.29E+00	1001	2.29E+00	1.80E+00
0.3	10	75	1.28E+00	1001	2.36E+00	1.86E+00
0.3	10	70	1.28E+00	1001	2.33E+00	1.82E+00
0.3	9	71	1.27E+00	1001	2.31E+00	1.79E+00
0.3	9	75	1.27E+00	1001	2.36E+00	1.83E+00
0.3	8	72	1.25E+00	1001	2.34E+00	1.78E+00
0.3	8	73	1.26E+00	1001	2.38E+00	1.83E+00
0.3	9	68	1.26E+00	1001	2.37E+00	1.82E+00
0.3	10	70	1.28E+00	1001	2.34E+00	1.83E+00
0.3	9	69	1.27E+00	1001	2.31E+00	1.78E+00
0.3	10	72	1.27E+00	1001	2.35E+00	1.83E+00
0.3	9	72	1.26E+00	1001	2.31E+00	1.80E+00
0.4	8	74	1.22E+00	1001	2.02E+00	1.68E+00
0.4	8	71	1.22E+00	1001	2.08E+00	1.73E+00
0.4	8	70	1.23E+00	1001	2.04E+00	1.71E+00
0.4	7	73	1.21E+00	1001	2.04E+00	1.68E+00
0.4	8	72	1.22E+00	1001	2.06E+00	1.72E+00
0.4	7	72	1.22E+00	1001	2.02E+00	1.67E+00
0.4	8	73	1.23E+00	1001	2.06E+00	1.73E+00
0.4	7	72	1.22E+00	1001	2.05E+00	1.68E+00
0.4	7	69	1.22E+00	1001	2.03E+00	1.69E+00
0.4	8	70	1.22E+00	1001	2.04E+00	1.70E+00
0.4	8	71	1.22E+00	1001	2.04E+00	1.72E+00
0.4	8	70	1.23E+00	1001	2.07E+00	1.73E+00
0.4	8	72	1.22E+00	1001	2.09E+00	1.71E+00
0.4	8	72	1.23E+00	1001	2.01E+00	1.70E+00
0.4	7	70	1.21E+00	1001	2.05E+00	1.65E+00
0.4	8	73	1.22E+00	1001	2.08E+00	1.69E+00
0.4	8	71	1.23E+00	1001	2.05E+00	1.73E+00
0.4	8	74	1.22E+00	1001	2.05E+00	1.73E+00
0.4	8	71	1.23E+00	1001	2.08E+00	1.73E+00
0.4	7	73	1.22E+00	1001	2.00E+00	1.66E+00
0.5	7	67	1.18E+00	1001	1.87E+00	1.67E+00
0.5	6	70	1.17E+00	1001	1.88E+00	1.64E+00
0.5	7	74	1.19E+00	1001	1.87E+00	1.64E+00
0.5	5	67	1.18E+00	474	1.85E+00	1.55E+00
0.5	7	71	1.18E+00	1001	1.83E+00	1.61E+00
0.5	6	74	1.17E+00	1001	1.86E+00	1.59E+00
0.5	7	71	1.19E+00	1001	1.85E+00	1.61E+00
0.5	7	73	1.19E+00	1001	1.85E+00	1.65E+00
0.5	6	69	1.18E+00	1001	1.86E+00	1.61E+00

0.5	7	70	1.18E+00	1001	1.85E+00	1.63E+00
0.5	6	74	1.18E+00	1001	1.86E+00	1.62E+00
0.5	7	68	1.18E+00	1001	1.92E+00	1.71E+00
0.5	6	71	1.18E+00	1001	1.85E+00	1.62E+00
0.5	5	73	1.17E+00	247	1.71E+00	1.38E+00
0.5	5	73	1.17E+00	1001	1.82E+00	1.53E+00
0.5	7	71	1.18E+00	1001	1.88E+00	1.66E+00
0.5	7	72	1.18E+00	1001	1.87E+00	1.64E+00
0.5	6	72	1.18E+00	1001	1.85E+00	1.60E+00
0.5	5	64	1.19E+00	99	1.61E+00	1.29E+00
0.5	6	67	1.18E+00	1001	1.85E+00	1.63E+00
0.6	5	69	1.14E+00	765	1.73E+00	1.56E+00
0.6	5	70	1.14E+00	771	1.71E+00	1.53E+00
0.6	4	66	1.14E+00	330	1.69E+00	1.47E+00
0.6	6	70	1.14E+00	1001	1.70E+00	1.52E+00
0.6	5	70	1.14E+00	557	1.67E+00	1.46E+00
0.6	5	74	1.14E+00	526	1.73E+00	1.51E+00
0.6	5	73	1.14E+00	496	1.67E+00	1.48E+00
0.6	5	74	1.14E+00	1001	1.73E+00	1.58E+00
0.6	5	70	1.14E+00	956	1.72E+00	1.55E+00
0.6	5	70	1.14E+00	218	1.66E+00	1.42E+00
0.6	5	68	1.14E+00	1001	1.73E+00	1.58E+00
0.6	3	58	1.13E+00	40	1.29E+00	8.91E-01
0.6	5	71	1.14E+00	1001	1.74E+00	1.54E+00
0.6	6	67	1.15E+00	383	1.66E+00	1.48E+00
0.6	5	70	1.14E+00	456	1.73E+00	1.54E+00
0.6	5	67	1.14E+00	687	1.72E+00	1.55E+00
0.6	6	72	1.15E+00	811	1.72E+00	1.56E+00
0.6	4	43	1.15E+00	34	1.29E+00	8.89E-01
0.6	4	64	1.16E+00	95	1.56E+00	1.26E+00
0.6	5	67	1.15E+00	493	1.69E+00	1.47E+00
0.7	5	65	1.12E+00	136	1.55E+00	1.39E+00
0.7	5	69	1.13E+00	182	1.59E+00	1.44E+00
0.7	5	63	1.11E+00	119	1.55E+00	1.40E+00
0.7	5	69	1.13E+00	260	1.56E+00	1.37E+00
0.7	4	72	1.12E+00	1001	1.62E+00	1.45E+00
0.7	5	70	1.12E+00	305	1.62E+00	1.51E+00
0.7	4	58	1.13E+00	94	1.53E+00	1.29E+00
0.7	4	73	1.12E+00	343	1.59E+00	1.41E+00
0.7	4	68	1.12E+00	185	1.57E+00	1.38E+00
0.7	4	55	1.11E+00	56	1.37E+00	1.02E+00
0.7	2	46	1.12E+00	31	1.26E+00	8.32E-01
0.7	4	54	1.15E+00	33	1.30E+00	8.61E-01
0.7	3	58	1.11E+00	114	1.57E+00	1.31E+00
0.7	3	49	1.11E+00	28	1.29E+00	9.15E-01
0.7	4	68	1.11E+00	475	1.64E+00	1.50E+00
0.7	4	59	1.11E+00	110	1.53E+00	1.41E+00
0.7	3	72	1.10E+00	85	1.45E+00	1.18E+00
0.7	5	65	1.13E+00	198	1.52E+00	1.31E+00
0.7	5	66	1.15E+00	122	1.45E+00	1.16E+00
0.7	4	70	1.12E+00	211	1.60E+00	1.46E+00
0.8	4	55	1.11E+00	112	1.51E+00	1.32E+00
0.8	3	52	1.11E+00	53	1.29E+00	9.03E-01
0.8	3	52	1.12E+00	63	1.45E+00	1.09E+00
0.8	4	72	1.10E+00	179	1.45E+00	1.19E+00
0.8	3	58	1.08E+00	82	1.52E+00	1.36E+00
0.8	6	49	1.13E+00	44	1.32E+00	9.21E-01
0.8	2	56	1.13E+00	25	1.25E+00	6.98E-01

0.8	4	67	1.10E+00	217	1.53E+00	1.44E+00
0.8	1	52	1.08E+00	30	1.35E+00	9.40E-01
0.8	5	66	1.10E+00	209	1.50E+00	1.34E+00
0.8	3	49	1.12E+00	33	1.36E+00	1.02E+00
0.8	3	42	1.09E+00	23	1.23E+00	7.12E-01
0.8	3	62	1.12E+00	65	1.52E+00	1.25E+00
0.8	5	50	1.13E+00	47	1.29E+00	8.96E-01
0.8	8	52	1.12E+00	53	1.43E+00	1.24E+00
0.8	1	52	1.09E+00	44	1.29E+00	8.76E-01
0.8	5	62	1.12E+00	89	1.46E+00	1.20E+00
0.8	4	58	1.09E+00	105	1.54E+00	1.40E+00
0.8	4	56	1.12E+00	32	1.22E+00	7.93E-01
0.8	4	71	1.10E+00	362	1.53E+00	1.38E+00
0.9	1	36	1.08E+00	21	1.25E+00	7.77E-01
0.9	1	38	1.04E+00	26	1.21E+00	7.72E-01
0.9	6	49	1.13E+00	33	1.24E+00	8.56E-01
0.9	3	53	1.09E+00	81	1.41E+00	1.17E+00
0.9	3	68	1.10E+00	85	1.46E+00	1.14E+00
0.9	3	53	1.13E+00	40	1.28E+00	8.48E-01
0.9	4	49	1.12E+00	32	1.32E+00	9.41E-01
0.9	8	50	1.10E+00	22	1.24E+00	8.05E-01
0.9	4	51	1.10E+00	68	1.42E+00	1.21E+00
0.9	3	45	1.12E+00	34	1.27E+00	8.25E-01
0.9	7	49	1.11E+00	48	1.31E+00	9.88E-01
0.9	4	57	1.11E+00	122	1.43E+00	1.22E+00
0.9	5	67	1.11E+00	198	1.44E+00	1.24E+00
0.9	6	41	1.11E+00	35	1.29E+00	9.54E-01
0.9	4	67	1.11E+00	82	1.45E+00	1.20E+00
0.9	3	54	1.10E+00	84	1.46E+00	1.30E+00
0.9	2	53	1.08E+00	79	1.44E+00	1.24E+00
0.9	3	64	1.08E+00	61	1.34E+00	1.03E+00
0.9	4	63	1.09E+00	65	1.37E+00	1.09E+00
0.9	2	34	1.09E+00	24	1.25E+00	8.33E-01
1.0	2	50	1.12E+00	29	1.33E+00	9.75E-01
1.0	3	43	1.12E+00	32	1.24E+00	7.56E-01
1.0	3	41	1.08E+00	24	1.19E+00	6.36E-01
1.0	5	53	1.20E+00	20	1.25E+00	7.65E-01
1.0	6	49	1.13E+00	43	1.35E+00	9.84E-01
1.0	3	51	1.09E+00	37	1.31E+00	9.43E-01
1.0	5	48	1.17E+00	37	1.31E+00	9.19E-01
1.0	4	51	1.13E+00	32	1.31E+00	8.88E-01
1.0	3	58	1.10E+00	62	1.35E+00	1.05E+00
1.0	1	44	1.09E+00	25	1.27E+00	8.10E-01
1.0	3	45	1.11E+00	41	1.33E+00	9.96E-01
1.0	4	53	1.11E+00	30	1.28E+00	8.80E-01
1.0	2	41	1.07E+00	39	1.26E+00	8.84E-01
1.0	6	45	1.14E+00	30	1.26E+00	8.06E-01
1.0	5	46	1.09E+00	31	1.29E+00	9.06E-01
1.0	2	58	1.11E+00	55	1.43E+00	1.18E+00
1.0	6	48	1.15E+00	28	1.25E+00	7.60E-01
1.0	4	49	1.13E+00	40	1.31E+00	9.52E-01
1.0	6	56	1.10E+00	60	1.34E+00	1.05E+00
1.0	4	39	1.15E+00	21	1.29E+00	7.93E-01