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EVOLUTIONARY MODELS
IN
STRUCTURED POPULATIONS

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Declaration

This thesis is entirely my own work, except where otherwise indicated.

This thesis is submitted to City University London for the Degree of Doctor of Philosophy, and no part of the work included in this thesis has been submitted in fulfilment of the award of any other Degree or qualification.

Abstract

Evolutionary dynamics have been traditionally studied in infinitely large homogeneous populations where each individual is equally likely to interact with every other individual. However, real populations are finite and characterised by complex interactions among individuals. In this work, the influence of the population structure on the outcome of the evolutionary process is explored.

Through an analytic approach, this study first examines the stochastic evolutionary game dynamics following the update rules of the invasion process, an adaptation of the Moran process, on finite populations represented by three simple graphs; the complete graph, the circle and the star graph. The exact formulae for the fixation probability and the speed of the evolutionary process under different conditions are derived, and the effect of the population structure on each of these quantities is studied.

The research then considers to what extent the change of the strategy update rules of the evolutionary dynamics can affect the evolutionary process in structured populations compared to the process in homogeneous well-mixed populations. As an example, the evolutionary game dynamics on the extreme heterogeneous structure of the star graph is studied analytically under different update rules. It is shown that in contrast to homogeneous populations, the choice of the update rules might be crucial for the evolution of a non-homogeneous population.

Although an analytic investigation of the process is possible when the contact structure of the population has a simple form, this is usually infeasible on complex structures and the use of various assumptions and approximations is necessary. This work introduces an effective method for the approximation of the evolutionary process in populations with a complex structure.

Another component of this research work involves the use of game theory for the modelling of a very common phenomenon in the natural world. The models developed examine the evolution of kleptoparasitic populations, foraging populations in which animals can steal the prey from other animals for their survival. A basic game-theoretical model of kleptoparasitism in an infinite homogeneous well-mixed population is extended to structured populations represented by different graphs. The features of the population structure that might favour the appearance of kleptoparasitic behaviour among animals are addressed.

In addition, a game-theoretical model is proposed for the investigation of the ecological conditions that encourage foraging animals to share their prey, a very common behaviour occurring in a wide range of animal species.

CHAPTER 1

Introduction

Evolution of populations has been an issue of great concern in the last centuries. Although evolution is a broad term, one can simply define it as a process by which populations change in the heritable characteristics over time. There have been various theories proposed in order to explain evolutionary changes in populations. In the middle of the 19^{th} century, Charles Darwin published a book, entitled 'On the Origin of Species by Means of Natural Selection', suggesting a revolutionary theory to explain evolution. Populations evolve by natural selection. Individuals occasionally mutate. Mutation is a genetic change due to an error in the reproduction process. These alterations generate differences among individuals in their ability to survive and reproduce. If the new individuals have a survival and reproductive advantage in their environment, then they reproduce at higher rates passing on their characteristics to their offspring. Disadvantageous individuals have a lower chance of survival and reproductive success and thus they are more likely to die out over time. Neutral mutant individuals, i.e. mutants that are neutral with respect to natural selection, might incorporate into the population by neutral drift. Natural selection acts on individuals, but only the population of individuals evolves over time. The time needed for a population to evolve depends on the nature of the population and might vary from minutes to millions of years. A population might be a human population, an animal population, a population of cells, multicellular organisms, molecules such as DNA and proteins, or any other evolving population. An outgrowth of Darwinian evolution is the cultural evolution which refers to cultural and social changes that occur over time (for example an erroneous imitation of behavioural traits, changes in the human language, ideas and opinions, strategic choices etc.).

Evolutionary game theory has been proven to be a powerful mathematical tool for the description and the study of the evolution of populations consisting of interacting individuals, including the evolution of populations of cells and viruses, the evolution of virulence in host-parasite interactions, the evolution of opinions through social interactions, and the evolution of populations of animals competing either over territory, mates, food or other biological resources, or for social status, using different strategies.

This chapter is an introductory chapter in game theory and evolutionary graph theory. It introduces the basic concepts of the classical and evolutionary game theory and some of the fundamental tools for the study of evolutionary game dynamics in finite homogeneous well-mixed populations of constant size through a stochastic approach. The famous Moran process is described and important quantities in the stochastic evolutionary process are considered. Then, evolutionary dynamics in structured populations and the basic idea of studying evolution of populations represented by graphs are discussed. Applications of game theory in the modelling of kleptoparasitism are also presented. At the end, the contributions and the outline of this work are provided.

1.1 Classical game theory

Game theory is the study of strategic decision-making of individuals. Game theory has a long history with origin in the 1920s when John von Neumann published a series of papers (summarised later in the book von Neumann and Morgenstern (1944)), although discussions of game theory had started much earlier, at the beginning of the 18th century. It has been applied to study individuals' behaviour in decision making problems in a wide variety of fields, including economics, biology, ecology, computer science, sociology, psychology and political sciences.

A *strategic game* is a model of interacting decision-makers, the *players*. At each stage of the game, each of the players has to take an *action*. The player's *strategy* determines the action taken at every possible stage of the game. Each player has a preference relation on the set of action profiles, which is represented by the so-called *payoffs*, i.e. the payoffs define a preference ordering. In other words, a payoff represents the motivation of a player to choose a specific strategy, the "award" of a choice. The payoff of each player might be affected not only by its own action but also by the action chosen by the other players that it is interacting with. In each case, the players try to attain the maximum possible payoff by choosing an appropriate action. The players might use pure strategies or mixed strategies. A *pure* strategy defines a specific action that a player will take at every possible stage of the game. The number of pure strategies can be either finite or infinite. A *mixed* strategy is a strategy according to which a player uses each of the available pure strategies with a certain probability. Since a probability can be any real number between 0 and 1, there is an infinite number of mixed strategies. A mixed strategy is usually represented by a row vector (probability vector) whose i^{th} entry is the probability that a player uses the i^{th} available pure strategy.

Depending on the nature of the strategic game, there are different ways to describe it. A commonly known type of game is the game in *normal form* (or strategic form). Games in this form consist of a finite number of players, a set of pure strategies available for each player to use, and the payoff function which determines the payoff of each player depending on its strategy and the strategy of its opponents. In normal form games all individuals play a strategy simultaneously, or individuals are not aware of the strategy of their opponents. When there are just two players and the number of available strategies for each player is finite, the game is usually called a *Bimatrix game*. In such games, the outcome of the payoff function can be represented by a matrix, the so-called *payoff matrix*. Assume two players, Player 1 and Player 2, where Player 1 has a finite strategy set $S = \{S_1, \dots, S_m\}$ and Player 2 a finite strategy set $T = \{T_1, \dots, T_n\}$. The column of the payoff matrix represents the strategic choices of the one player and the row the strategic choices of the other. Each element in row i and column j of the matrix is an ordered pair (s_i, t_j), where s_i represents the payoff received by the "row player" and t_j the payoff received by the "column player" when the row player plays strategy S_i and the column player plays strategy T_j. For every possible combination of pure strategies S_i, $i \in [1,m]$, and T_j, $j \in [1,n]$, there is a corresponding pair of numbers (s_i, t_j). This game can be represented by the following payoff matrix

$$\begin{array}{cc|ccccc}
 & & \multicolumn{5}{c}{\text{Player 2 (Column Player)}} \\
 & \text{Strategy} & T_1 & \dots & T_j & \dots & T_n \\
\cline{2-7}
 & S_1 & (s_1,t_1) & \dots & (s_1,t_j) & \dots & (s_1,t_n) \\
\text{Player 1} & \vdots & \vdots & \dots & \vdots & \dots & \vdots \\
\text{(Row Player)} & S_i & (s_i,t_1) & \dots & (s_i,t_j) & \dots & (s_i,t_n) \\
 & \vdots & \vdots & \dots & \vdots & \dots & \vdots \\
 & S_m & (s_m,t_1) & \dots & (s_m,t_j) & \dots & (s_m,t_n)
\end{array} . \tag{1.1}$$

In the case of *symmetric games*, i.e. games where both players have the same strategic choices, $S = \{S_1 \dots S_n\}$, and the payoff obtained by using each strategy is irrespective of the player that uses it, the game can be described by a square $n \times n$ payoff matrix, whose element in the i^{th} row and j^{th} column represents the payoff of the row player when using strategy S_i against the column player that uses strategy S_j.

For example, in a two-player symmetric game in normal form where there are two possible strategies for each player, A and B (such games are also called 2×2 games), the interactions between the individuals can be described by the payoff matrix

$$\begin{array}{c|cc} & \mathrm{A} & \mathrm{B} \\ \hline \mathrm{A} & a & b \\ \mathrm{B} & c & d \end{array} \,. \tag{1.2}$$

An individual playing strategy A (A individual) obtains a payoff a when interacting with another individual playing A and a payoff b when interacting with an individual playing B (B individual). Similarly, an individual playing strategy B obtains payoffs c and d when interacting with an individual playing A and an individual playing B, respectively.

In this work, we will consider two-player symmetric games in normal form.

1.1.1 Dominant strategies and Nash equilibria

In this section, we present in a simple way some important definitions and main solution concepts of the classical game theory.

The *best response* strategy is the strategy (or strategies) that when it is used against a given strategy offers the highest possible payoff. If this strategy is unique, i.e. it results in a strictly higher payoff against a given strategy then it is called the *strict* best response to that strategy.

A *dominant strategy* (*strictly* dominant strategy) is a strategy that is a (strict) best response to every other strategy, i.e. it results in the highest payoff compared to the other available strategies no matter what the opponent does.

A *Nash equilibrium* (Nash, 1951) is a set of strategies consisting of a strategy for each player. The strategy of each player is a best response to the other players' strategy, i.e. if any of the players chooses a different strategy and the strategies of the other players remain unchanged, its payoff will either remain the same or decrease. If the decrease in payoff is the only possible result of such a choice, then the set of strategies is called a *strict* Nash equilibrium. If a player has a strictly dominant strategy, then this strategy is obviously the one that is used in the Nash equilibria of the game. In mathematical terms, in a two-player symmetric game, a strategy i is a Nash equilibrium if $E(i,i) \geq E(j,i)\ \forall j$, and a strict Nash equilibrium if $E(i,i) > E(j,i)\ \forall j \neq i$, where $E(X,Y)$ represents the payoff for playing strategy X against strategy Y. A game can have either a pure-strategy or a mixed-strategy Nash equilibrium. Although in general pure strategy Nash equilibria may not exist, it is proved (Nash, 1951) that in a finite game (a game that has a finite number of players and actions) there always exists a Nash equilibrium if individuals can use mixed strategies.

Two concepts which are sometimes important are those of Pareto efficiency and risk-dominance. A strategy is called *Pareto efficient* (or Pareto optimal) if there is no any other strategy that can improve the payoff of a player without reducing the payoff of at least one other player. Note that a Nash equilibrium is not necessarily Pareto efficient; there might be sets of strategies which may result in better outcomes for both players but are not Nash equilibria. A strategy is called *risk dominant* if it has the largest basin of attraction, i.e. it becomes more preferable in cases where the uncertainty about the strategy of the opponents increases. For example, in a 2×2 game described by the payoff matrix (1.2) where strategies A and B are strict Nash equilibria, i.e. $a > c$ and $b < d$, if $a > d$ then A is Pareto efficient, but if $a+b < c+d$ then B is risk-dominant, given that each player assigns probability 0.5 to each of the strategies A and B. It is often interesting to consider when selection favours the Pareto efficient Nash equilibrium over the risk dominant Nash equilibrium, for example in coordination games (see Sections 1.3.3 and 3.4.2).

1.2 Evolutionary game theory

In contrast to the classical game theory where individuals play a static game and choose the strategy that offers them the maximum possible payoff, given that all individuals behave rationally, evolutionary game theory is a dynamic theory which studies the evolution of populations where individuals interact repeatedly with other individuals. The different strategies might be thought of as different types of individuals and the payoffs obtained by each individual when interacting with other individuals are interpreted as *fitness*, which determines the reproductive and survival success. Therefore, depending on the payoff values, the fitness of each individual might be either constant (*constant fitness*) or dependent on the frequency (relative proportion) of the other types of individuals in the population (*frequency dependent fitness*).

The evolutionary process is mainly determined by the selection and mutation process. In terms of the evolutionary game theory, under selection individuals with the highest payoff (and thus fitness) are more likely to pass on their traits (genetic or cultural) to subsequent generations. Consequently, the frequency of these individuals increases. Similarly, the frequency of the less successful individuals decreases. Mutation can be interpreted as a change in the strategic choice of individuals in subsequent generations.

Evolutionary game dynamics have been traditionally studied in infinitely large unstructured populations where every individual is equally likely to meet every other individual. There are two traditional approaches to evolutionary game theory. The first is the approach of Maynard Smith and Price (1973) who introduced the concept of an Evolutionarily Stable Strategy. The second approach studies the variation in the frequency of the different types of individuals over time through the construction of a dynamical system of equations, the replicator equations.

1.2.1 Evolutionarily Stable Strategies

A strategy is an *Evolutionarily Stable Strategy* (ESS) (Maynard Smith and Price, 1973) if a population adopting that strategy cannot be invaded by a small number of individuals playing any alternative strategy (mutant strategy), i.e. if it is stable with respect to changes in strategic choices of individuals. But let us consider the definition of an ESS in mathematical terms.

Consider an infinitely large resident population where all individuals use a strategy (pure or mixed), R. Assume that initially all individuals have a background (initial) fitness equal to f_b and let $\Delta f(X,Y)$ be the change in fitness for an individual of a subpopulation that plays strategy X (X individual) when interacting with an individual of a subpopulation that plays strategy Y (Y individual) (this is equal to the payoff of an X individual when playing against a Y individual). The expected fitness of an individual of a population where all individuals use strategy R, is

$$f_R = f_b + \Delta f(R,R). \tag{1.3}$$

Assume that this population is invaded by a very small proportion ε of mutant individuals that play strategy M. In this case, the expected fitness of a random R individual of the population is given by

$$f_R = f_b + (1-\varepsilon)\Delta f(R,R) + \varepsilon \Delta f(R,M), \tag{1.4}$$

and the expected fitness of a random individual playing the mutant strategy is

$$f_M = f_b + (1-\varepsilon)\Delta f(M,R) + \varepsilon \Delta f(M,M). \tag{1.5}$$

Mutant individuals playing strategy M cannot invade a population of individuals playing strategy R, if

$$f_R > f_M, \tag{1.6}$$

for all the possible strategies M $\neq$ R. Since ε is a very small proportion close to zero, this is true if

$$\Delta f(R,R) > \Delta f(M,R) \text{ or} \tag{1.7}$$

$$\Delta f(R,R) = \Delta f(M,R) \text{ and } \Delta f(R,M) > \Delta f(M,M). \tag{1.8}$$

A strategy R is an ESS if either the condition (1.7) or the condition (1.8) holds for all the available strategies M, M $\neq$ R. In words, the condition (1.7) means that a very small proportion of mutant individuals playing strategy M cannot invade a population of resident individuals playing R if an individual playing strategy R compared with an individual playing strategy M has an advantage when both play against an individual that plays R, i.e. if R is a strict best response to itself. The condition (1.8) means that even if a resident individual does equally well with a mutant when playing against a resident, the mutants cannot invade the population as long as a resident does better when playing against a mutant, i.e. if R is a better response to M, than M to itself.

It follows from conditions (1.7) and (1.8) that a necessary condition for a strategy to be an ESS is for it to be a Nash equilibrium, and thus every ESS is a Nash equilibrium. But note that a Nash equilibrium is not necessarily an ESS. If a strategy is a strict Nash equilibrium, then condition (1.7) must hold, and thus every strict Nash equilibrium is an ESS.

It should be noted that there might be conditions under which there are many possible ESSs simultaneously and the population stabilised into one of these. On the other hand, there might be circumstances in which there are no ESSs.

A limitation of the evolutionarily stable strategy concept is that it begins from the state in which all the members of the population play the same strategy without considering how this state has been reached. In addition, it considers only the stability of the population strategy in isolated changes in the strategic choices of a very small proportion of the population, without considering any mutations during the evolutionary process. Furthermore, the concept holds as long as the population size is infinite, and population structure and stochasticity are ignored.

1.2.2 Replicator Dynamics

In contrast to the concept of evolutionarily stable strategies, the *replicator dynamics* describe how the frequencies of strategies within a population change in time.

Consider a homogeneous well-mixed population of infinite size where individuals can use only pure strategies from a finite set $S = \{S_1, ..S_n\}$. Let us consider the simplest case where individuals can use either strategy A or strategy B. The game played between the individuals is described by the payoff matrix (1.2). The expected fitnesses of individuals playing strategy A and B are given respectively by

$$f_A = f_b + x_A a + x_B b, \tag{1.9}$$

$$f_B = f_b + x_A c + x_B d. \tag{1.10}$$

x_A is the frequency of individuals playing strategy A, and x_B the frequency of individuals playing B. The average fitness of the population is thus given by

$$F = x_A f_A + x_B f_B. \tag{1.11}$$

Since the population consists only of individuals that play either strategy A or strategy B, $x_A + x_B = 1$. The evolution of the population can be described by the following dynamic equation,

$$\dot{x}_A = x_A (f_A - F). \tag{1.12}$$

This is called the *replicator equation* (Taylor and Jonker, 1978; Hofbauer *et al.*, 1979; Hofbauer and Sigmund, 1998, 2003).

From equation (1.12), it is obvious that at any time, if the fitness of individuals playing A is higher than the average fitness of the population, their frequency will increase. If their fitness is lower than the average fitness of the population, then their frequency will decrease. Hence, the replicator equation describes the deterministic selection process where more successful strategies spread in the population. As in the approach discussed in the previous section, mutation is not considered.

Substituting equations (1.9)–(1.11) into (1.12) we obtain

$$\begin{aligned} \dot{x}_A &= x_A(1 - x_A)(f_A - f_B) && (1.13) \\ &= x_A(1 - x_A)\big(x_A(a - b - c + d) + b - d\big). && (1.14) \end{aligned}$$

From (1.14) we see that there are three generic equilibrium points,

$$x_A^* = 0, \tag{1.15}$$

$$x_A^* = 1, \tag{1.16}$$

$$x_A^* = \frac{b - d}{b + c - a - d}, \quad \text{for } a > c \text{ and } b < d, \text{ or for } a < c \text{ and } b > d. \tag{1.17}$$

Note that as in the ESS concept, the background fitness of individuals is irrelevant and only the values of the payoffs matter.

There are three distinct generic scenarios for the evolutionary process:

i. *Dominance*: In this case, either strategy A is always better no matter what the opponent does and thus the equilibrium point $x_A^* = 1$ is stable (the case where $a > c$ and $b > d$), or B is always better than A and thus the equilibrium point $x_A^* = 0$ is stable (the case where $a < c$ and $b < d$). In each case, the better strategy is a strict Nash equilibrium and therefore an ESS.

ii. *Bistability*: The two equilibrium points $x_A^* = 0$ and $x_A^* = 1$ are both strict Nash equilibria, and thus strategies A and B are both ESSs. The equilibrium point given by (1.17) is unstable. Evolution will result in the fixation of As when their frequency is above x_A^*, and in their extinction when their frequency is below x_A^*. This is the case where $a > c$ and $b < d$.

iii. *Coexistence*: The interior equilibrium point (1.17) is stable while the points $x_A^* = 0$ and $x_A^* = 1$ are both unstable. This is the case where $a < c$ and $b > d$.

In the non-generic cases where $a \geq c$ and $b > d$, or $a > c$ and $b \geq d$, strategy A also dominates B. In the cases where $a \leq c$ and $b < d$, or $a < c$ and $b \leq d$, B also dominates A.

In the non-generic case where $a = c$ and $b = d$, i.e. $f_A = f_B$ for all values of x_A, the two strategies do equally well and thus the frequency distribution of the strategies remains constant. This case is called the *neutral case*. Although this case is not much of interest in the replicator dynamics, as we will see in Chapters 2 and 3, it is an interesting and important case in the stochastic evolutionary dynamics of finite populations.

Note that constant selection, where individuals have constant fitness independent of the interactions with other individuals and thus of the composition of the population, can be obtained in the special case where $a = b$ and $c = d$.

The replicator equation can be generalised for n different strategic types of individuals. Consider a population where each individual interacts in equal likelihood with any other individual and can use one of the n available pure strategies of the set S. The change of the frequencies x_i, $i \in [1,n]$, of the different types of individuals over time is described by the equations

$$\dot{x}_i = x_i(f_i - F), \tag{1.18}$$

where f_i is the expected fitness of an individual that uses strategy S_i and is given by $f_i = f_b + \sum_{j=1}^{n} x_j \Delta f(S_i, S_j)$, and F is the average fitness of the entire population and is given by $F = \sum_{i=1}^{n} x_i f_i$.

1.3 Some classical games

In this section, we present some of the classical games that have been widely studied and applied in different fields.

1.3.1 The Hawk–Dove game

The *Hawk–Dove* game (Maynard Smith and Price, 1973; Maynard Smith, 1982) is possibly the most classic evolutionary game. This game has been used extensively for the modelling of competition of animals over food, mates, territories, and other biological resources. According to this game, individuals interact with each other over a resource of value V by playing either aggressively using the Hawk strategy (H) or non-aggressively using the Dove strategy (D). If two individuals playing Hawk meet, a fight takes place. At the end of the fight, the winner of the game gets a payoff V while the loser pays a cost C. Therefore, the two players obtain a payoff on average equal to $(V-C)/2$. If two Doves meet, they either equally share the resource (if divisible) or with equal probability one of the two takes the whole resource with no cost. Thus, in this case Doves obtain an average payoff equal to $V/2$. If a Hawk meets a Dove, the Dove retreats leaving the resource to the Hawk without any cost, and thus the Hawk obtains a payoff, V, while the Dove gets nothing. This game is described by the following payoff matrix:

$$\begin{array}{c|cc} & \mathrm{H} & \mathrm{D} \\ \hline \mathrm{H} & a=\frac{V-C}{2} & b=V \\ \mathrm{D} & c=0 & d=\frac{V}{2} \end{array} . \tag{1.19}$$

It is clear that since $b > d$, the Dove strategy is never evolutionarily stable because a population of Doves can always be invaded by a Hawk. If the value of the resource outweighs the cost of the fight, i.e. if $V > C \Rightarrow a > c$, since $b > d$, an individual always does better by playing the Hawk strategy no matter what the opponent does (the Hawk strategy is strictly dominant). Thus, in an infinite homogeneous well-mixed population the Hawk strategy is the unique pure ESS. Hawk is also the unique pure ESS when $V = C$, because $b > d$. If $V < C \Rightarrow a < c$, it is better to play Dove when Hawks are common. Since it is better to play Hawk when Doves are common, this leads to an evolutionarily stable mixed strategy. Assume that with probability $p \in (0,1)$ individuals use the Hawk strategy, and with probability $1-p$ they use the Dove strategy. In order a mixed strategy $(p^*, 1-p^*)$ to be an ESS, in a population playing strategy $(p^*, 1-p^*)$, the fitness of an individual playing the Hawk strategy must be equal to the fitness of an individual playing the Dove strategy, i.e.

$$p^* \frac{V-C}{2} + (1-p^*)V = p^*\,0 + (1-p^*)\frac{V}{2}. \tag{1.20}$$

Solving for p^* we obtain that $p^* = V/C$. It is easy to show that an individual playing the mixed strategy $(V/C, 1-V/C)$ in a population playing any other strategy $(p, 1-p)$, $p \in [0,1]$, has a higher fitness than an individual of that population. Hence, according to condition (1.8), there is a unique mixed ESS where individuals play Hawk with probability V/C and Dove with probability $1-V/C$. The mixed ESS can also be found by using the approach in Section 1.2.2.

Note that here we assumed a monomorphic population where all individuals choose randomly between the pure strategies according to a given probability distribution, and thus all individuals play the same mixed strategy. A similar method could be followed in the case of a polymorphic population where individuals use different pure strategies. In this case, the mixture of strategies is a polymorphic mixture of individuals where a proportion of the population equal to V/C uses the pure Hawk strategy and a proportion $1-V/C$ uses the pure Dove strategy. Mathematically, in infinite unstructured populations, the two cases are equivalent because in either case an individual of the population has a probability p of meeting an individual playing Hawk and a probability $1-p$ of meeting an individual playing Dove.

1.3.2 The Prisoner's Dilemma game

The *Prisoner's Dilemma* (Axelrod, 1984; Poundstone, 1992) is one of the most popular games in game theory and has been commonly applied for the study of the evolution of cooperation.

Assume a population where individuals either cooperate (use strategy C) or defect (use strategy D). Mutual cooperation results in a payoff R (reward) while mutual defection results in a payoff P (punishment). T (temptation) is the payoff obtained by a defector against a cooperator and S (sucker's payoff) is the payoff of a cooperator against a defector. The game is described by the payoff matrix

$$\begin{array}{c|cc} & \mathrm{C} & \mathrm{D} \\ \hline \mathrm{C} & R & S \\ \mathrm{D} & T & P \end{array}\,. \tag{1.21}$$

In the Prisoner's Dilemma, the order of the elements of the payoff matrix (1.21) is $T > R > P > S$. Thus, in this game, mutual cooperation results in a higher payoff than mutual defection and therefore a population of all cooperators does better than a population of all defectors. However, since $T > R$ and $P > S$, it is always better to defect regardless of what the partner does and thus mutual defection is the unique Nash equilibrium, and defection is the only ESS.

In its simplest form, the Prisoner's Dilemma can be described as the game where a cooperator provides a benefit B to its partner at a cost C to itself. A defector just receives the benefit from a cooperator without paying any cost. The payoff matrix of the game in this form is

$$\begin{array}{c|cc} & \mathrm{C} & \mathrm{D} \\ \hline \mathrm{C} & B-C & -C \\ \mathrm{D} & B & 0 \end{array}, \tag{1.22}$$

with $B > C > 0$.

1.3.3 Coordination games

A *coordination game* is a game with multiple pure strategy Nash equilibria. In a two strategy game described by the payoff matrix (1.2), a coordination game is defined by $a > c$ and $b < d$, and thus strategies A and B are both Nash equilibria. The replicator dynamics also predicts an unstable interior equilibrium where the population fraction of A individuals, x_A^*, is given by (1.17). Usually, one of the strategies in this game is Pareto efficient while the other one is risk dominant.

A famous coordination game is the so-called Stag Hunt game (Skyrms, 2004) where $a > c > d > b$.

1.3.4 The Snowdrift game

The *Snowdrift game* (Sugden, 1986) is a game described by the payoff matrix (1.21) with payoff ranking $c > a > b > d$. Hence, in this game the best strategy depends on what the opponent plays and, as in the Hawk–Dove game for $C > V$, it is better to do the opposite of what the opponent does. The Snowdrift game is actually a version of the Hawk–Dove game described in Section 1.3.1 but it has been widely used in this form for the study of the evolution of cooperation, where strategy A is described as the cooperative strategy and B as the defective strategy.

1.4 Stochastic evolutionary dynamics in finite homogeneous populations – The Moran process

The traditional evolutionary game theory has provided important insights into the evolutionary game dynamics. However, both the concept of evolutionarily stable strategies and the replicator dynamics describe a selection process in infinitely large populations and they are usually not effective to describe the dynamics of real populations of finite size, especially in cases where the size of the population is small. A better understanding of the evolution of finite populations requires a stochastic approach.

The *Moran process* is a classical stochastic model originally formulated for modelling population genetics (Moran, 1958, 1962) and later has been applied for the study of evolutionary game dynamics in finite populations (Nowak *et al.*, 2004; Taylor *et al.*, 2004). It is a process which has been commonly used for the study of the evolution of finite homogeneous populations consisting of two types of individuals, where each individual is equally likely to interact with every other individual. Assume a finite population of size N which consists of two types of individuals. According to this process, in each time step a random individual reproduces an offspring of the same type and a random individual dies. Thus, since in each step there is exactly one birth event and exactly one death event, the population size remains constant. In the case where the two types of individuals in the population have different fitness the process is described as follows: in each time step, a random individual of type T_i is chosen for reproduction with probability proportional to its fitness, i.e. with probability

$$p_i = \frac{i f_i}{\sum_{j=1}^{N} j f_j}, \tag{1.23}$$

where f_i denotes the fitness of an individual of type T_i and i the number of the individuals of that type. Hence, the type of individual which has the fitness advantage will be selected for reproduction with higher probability. For example, for two types of individuals, A and B, an A individual is chosen for reproduction with probability $i f_A/(i f_A + (N-i) f_B)$, where i is the number of individuals of type A. The individual chosen for reproduction produces an identical offspring which replaces a randomly chosen individual (Figure 1.1). It should be noted that depending on the nature of the process, the offspring can replace its parent or not. In this work, we assume that the offspring cannot replace its parent. Due to the finiteness of the population size and since in the process there are no mutations, eventually one of the two types of individuals will replace all the individuals of the other type and fixate in the population.

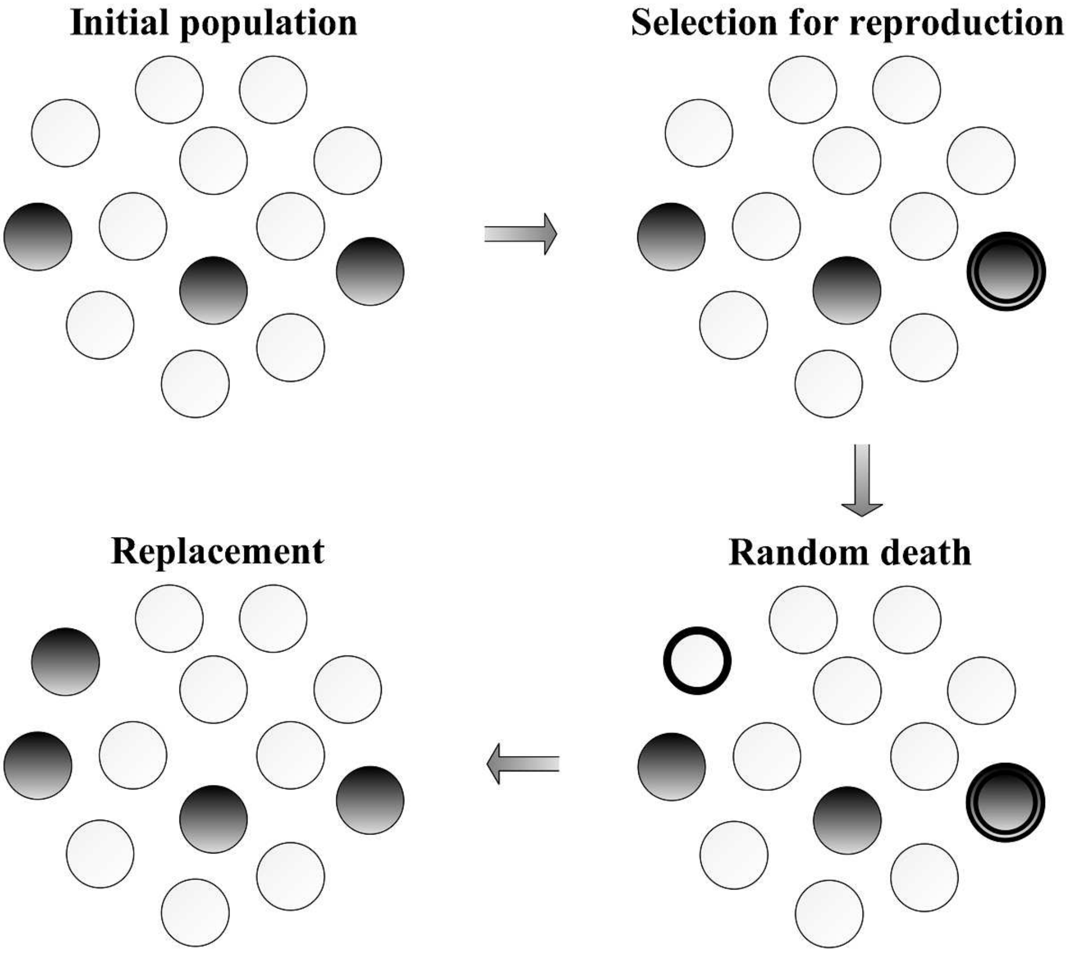


Figure 1.1: The Moran process with frequency dependent fitness. A finite population consists of two types of individuals, A and B. In each time step, an individual is randomly selected for reproduction with probability proportional to its fitness. An individual is chosen for death at random. An identical offspring of the individual chosen for reproduction replaces the dead individual. Hence, in each time step the population size remains constant.

So, there are some reasonable questions: What is the probability that a particular type will fixate? How long will it take to fixate given that this will happen? How long will it take for one of the two types to fixate?

Consider a population consisting of two types of individuals, X and Y. The *fixation probability* of type X is the probability that at the end of the evolutionary process the population will consist only of X individuals, i.e. the probability that X individuals will spread over the whole population and fixate. The *mean absorption time* (or unconditional fixation time) is the mean number of time steps needed to reach one of the two absorbing states of the dynamics, i.e. the required time for the process to end up either in the state where all individuals are of type X or in the state where all individuals are of type Y. The *mean fixation time* (or conditional fixation time) of X individuals is the number of time steps required for X individuals to take over the entire population, given that this will happen. Another quantity of potential interest that we introduce in this work is the *mean number of transitions* to absorption or fixation, where the number of transitions is defined as in the time, except that events where the population size of one type of individuals (and thus that of the other) is unchanged are not counted.

Expressions for the fixation probability as well as the mean fixation time were derived in Karlin and Taylor (1975). The fixation probability has later been considered in populations of finite size (Nowak *et al.*, 2004; Taylor *et al.*, 2004). Complete derivations of the formulae of the fixation probability and the mean time to absorption and fixation in a homogeneous population of finite size can be found in Antal and Scheuring (2006) and Traulsen and Hauert (2009). In Appendix A we reproduce these derivations and in some cases we present alternative formulae. Note that these formulae can be applied to stochastic evolutionary processes where there is no mutation and in each time step the number of individuals of one type increases by one, decreases by one or remains the same, and thus the population size remains constant.

Consider a population of size N with two types of individuals, A and B. According to the Moran process, the number of A individuals in each time step can increase by one, decrease by one or remain the same, with some probabilities that depend only on the current state of the system. Hence, the process is a Markov process, which is essentially a discrete random walk on states $0 \leq i \leq N$ with absorbing boundaries. The transition matrix of the process is a tri-diagonal matrix with entries

$$p_{i,i+1} = \frac{i f_A}{i f_A + (N-i) f_B} \cdot \frac{N-i}{N-1}, \quad 1 \leq i \leq N-1, \tag{1.24}$$

$$p_{i,i-1} = \frac{(N-i) f_B}{i f_A + (N-i) f_B} \cdot \frac{i}{N-1}, \quad 1 \leq i \leq N-1, \tag{1.25}$$

$$p_{i,i} = 1 - p_{i,i+1} - p_{i,i-1}, \qquad 1 \leq i \leq N-1, \tag{1.26}$$

and zero everywhere else. Here, $p_{i,j}$ is the element in the i^{th} row and j^{th} column of the transition matrix and denotes the transition probability from the state with i A individuals to the state with j A individuals. At the absorbing states, $p_{0,0} = p_{N,N} = 1$.

The fixation probability of $i \in [1,N]$ A individuals in a finite well-mixed population of B individuals, ${}^{A}P_i$, is given by (see Appendix A.1)

$${}^{A}P_i = \frac{1 + \sum\limits_{j=1}^{i-1} \prod\limits_{k=1}^{j} q_k}{1 + \sum\limits_{j=1}^{N-1} \prod\limits_{k=1}^{j} q_k}, \tag{1.27}$$

where q_k is the ratio of the probability of the number of A individuals being decreased by one, $p_{k,k-1}$, and the probability of the number of A individuals being increased by one, $p_{k,k+1}$, i.e. $q_k = p_{k,k-1}/p_{k,k+1}$. Clearly, the probability of i A individuals dying out, i.e. the fixation probability of $N-i$ B individuals, ${}^{B}P_i$, is given by ${}^{B}P_i = 1 - {}^{A}P_i$ which leads to

$$ {}^{B}P_i = \frac{\sum\limits_{j=i}^{N-1} \prod\limits_{k=1}^{j} q_k}{1 + \sum\limits_{j=1}^{N-1} \prod\limits_{k=1}^{j} q_k}. \tag{1.28}$$

The (average) fixation probability of a single individual playing strategy X, ${}^{X}P_1$, will be denoted by ${}^{X}P$.

In the case where each of A individuals has relative constant fitness equal to r, when compared to the fitness of a B individual, the transition probabilities are

$$p_{i,i+1} = \frac{ir}{ir+N-i} \cdot \frac{N-i}{N-1}, \quad 1 \le i \le N-1, \tag{1.29}$$

$$p_{i,i-1} = \frac{N-i}{ir+N-i} \cdot \frac{i}{N-1}, \quad 1 \le i \le N-1, \tag{1.30}$$

$$p_{i,i} = 1 - p_{i,i+1} - p_{i,i-1}, \quad 1 \le i \le N-1, \tag{1.31}$$

$$p_{0,0} = p_{N,N} = 1, \tag{1.32}$$

and equal to zero in any other case. In this case $q_k = 1/r$, and thus from the formula (1.27) we obtain that in the Moran process the fixation probability of $i \in [0,N]$ A individuals which have a constant fitness r times higher than that of B individuals, ${}^{A}\mathrm{P}_{\mathrm{M}i}$, is given by the simple formula

$$ {}^{A}\mathrm{P}_{\mathrm{M}i} = \frac{1-r^{-i}}{1-r^{-N}}, \quad r \neq 1 \tag{1.33}$$

(the fixation probability of a single mutant A in the Moran process will be denoted by ${}^{A}\mathrm{P}_{\mathrm{M}}$). Hence, in contrast to the deterministic replicator dynamics (see Section 1.2), although individuals with fitness $r > 1$ are favoured by selection (their fixation probability is higher than that of a neutral individual, $1/N$) their fixation is not certain, even in an infinitely large population. Similarly, although selection opposes the fixation of individuals with fitness $r < 1$ (their fixation probability is less than $1/N$) and thus their extinction is more likely, this is not certain. This occurs due to the fact that even the fittest individual might not be chosen for reproduction and even the least fit individual might be chosen for reproduction. This random effect is called *random drift* and is very important in the evolution of finite populations, especially when the population size is small. For $r = 1$, we have the case of so-called *neutral drift*, where all individuals have the same fitness. In this case, although there is no natural selection, the frequencies A and B individuals will drift until one strategy takes over the entire population. The fixation probability of i As in this case is equal to i/N. This should be expected, since every individual can reproduce or die with equal probability. Thus, every single individual has probability $1/N$ to take over the entire population and fixate no matter its type; since there are i individuals of type A, their probability to fixate is i/N.

The mean time to absorption when $i \in [1,N]$ A individuals are introduced in a population of B individuals, T_i, is given by (see Appendix A.2)

$$T_i = {}^{A}P_i \sum_{j=1}^{N-1} \frac{1}{p_{j,j+1}} \sum_{l=j}^{N-1} \prod_{k=j+1}^{l} q_k - \sum_{j=1}^{i-1} \frac{1}{p_{j,j+1}} \sum_{l=j}^{i-1} \prod_{k=j+1}^{l} q_k. \tag{1.34}$$

The (average) time to absorption starting from a single individual playing strategy X will be denoted by ${}^{X}T$.

The fixation time of $i \in [1,N]$ A individuals in a population of Bs, ${}^{A}F_i$, is given by (see Appendix A.3)

$${}^{A}F_i = \sum_{j=1}^{N-1} \frac{{}^{A}P_j}{p_{j,j+1}} \sum_{l=j}^{N-1} \prod_{k=j+1}^{l} \frac{p_{k,k-1}}{p_{k,k+1}} - \frac{1}{{}^{A}P_i} \sum_{j=1}^{i-1} \frac{{}^{A}P_j}{p_{j,j+1}} \sum_{l=j}^{i-1} \prod_{k=j+1}^{l} \frac{p_{k,k-1}}{p_{k,k+1}}. \tag{1.35}$$

The (average) fixation time of a single individual playing strategy X, ${}^{X}F_1$, will be denoted by ${}^{X}F$. The derivation of the mean time to fixation of B individuals can be found in Antal and Scheuring (2006) and Traulsen and Hauert (2009). However, these can also be derived from the formula (1.35) by symmetry arguments.

The above formulae are effectively a re-organisation of the ones in Traulsen and Hauert (2009).

Note that in the Moran process, the mean fixation time of a single A individual when it is introduced into a population of Bs, ${}^{A}F$, is the same as the mean fixation time of a single B when it is introduced into a population of As, ${}^{B}F$, for every intensity of selection and for all games. Thus, ${}^{A}F = {}^{B}F$ irrespective of which of the two types of individuals has the highest chance to fixate into a population of the other type. This does not hold in the cases where more than one individual of one type invades in a population of individuals of the other type (Taylor *et al.*, 2006).

In order to find the mean number of transitions before absorption occurs, as well as the mean number of transitions before the fixation of A individuals, we consider a process where in each of the time steps we have a transition from one state to a different state, i.e. in each time step the number of A individuals either increases or decreases by one. The transition matrix of this process is a square matrix where only the entries below and the entries above the main diagonal can be non-zero. The elements of the transition matrix are

$$\pi_{i,i+1} = \frac{f_A}{f_A + f_B}, \quad 1 \leq i \leq N-1, \tag{1.36}$$

$$\pi_{i,i-1} = \frac{f_B}{f_A + f_B}, \quad 1 \leq i \leq N-1, \tag{1.37}$$

and zero everywhere else.

The mean number of transitions before absorption and fixation of A individuals occurs, starting from $i \in [1, N]$ As, is given by the formulae (1.34) and (1.35), respectively, where $p_{i,i+1} = \pi_{i,i+1}$ and $p_{i,i-1} = \pi_{i,i-1}$.

1.5 The effect of spatial structure on the outcome of the evolutionary process

As we have seen in the previous sections, the traditional theory of evolutionary game dynamics is based on the assumption that populations are infinitely large and well-mixed. However, real populations, ranging from biology and ecology to computer science and socio-economics, are of finite size and exhibit some non-homogeneous structure where any two individuals have not the same probability to meet. For example, individuals might have a higher probability to interact with neighbouring individuals than with distant individuals.

At its simplest, the spatial effects on the evolutionary game dynamics have been considered by assuming that the individuals of the population are distributed over a spatial array and interact with their nearest neighbours (see for example, Nowak and May, 1992, 1993; Nowak, 2006; Killingback and Doebeli, 1996; Szabó and Tőke, 1998; Hauert, 2002; Hauert and Doebeli, 2004; Szabó and Fáth, 2007). This might be a one-dimensional array, a two-dimensional array (e.g., triangular lattice, square lattice, hexagonal lattice) or higher dimensional array (e.g., cubic). However, biologically only lattices of dimension one, two and three are of interest. Each individual adopts a strategy from a finite number of strategies available to use. Individuals update their strategy following either deterministic or stochastic update rules. In the deterministic evolutionary dynamics (in discrete time), in every generation each individual updates its strategy and adopts the strategy which has obtained the highest total payoff among its strategy and its neighbours' strategies. The total payoff of

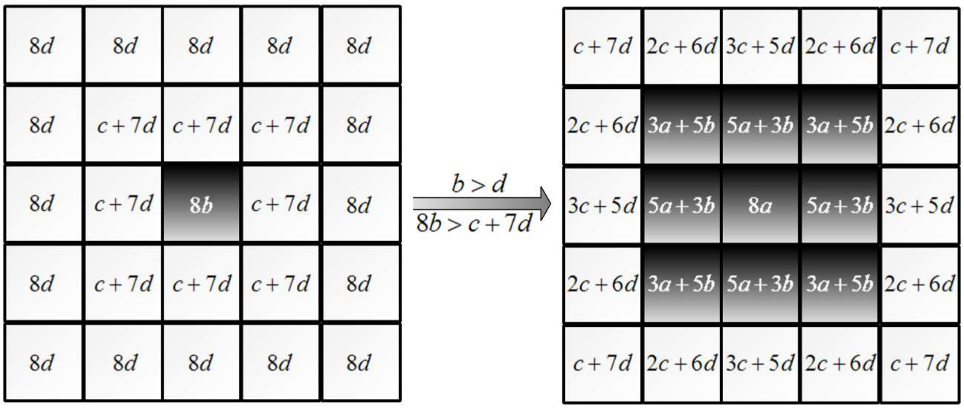


Figure 1.2: A spatial evolutionary game. Here, individuals of the population occupy the cells of a square lattice and each of them interacts with its 8 neighbours. The game played among the individuals is described by the payoff matrix (1.2). The payoff of each individual at the end of each round is the sum of the payoffs obtained by the games played with each of its neighbours in the round. Every individual compares its payoff with that of its neighbours and adopts the strategy which resulted in the highest payoff. The figure shows the neighbourhood of an individual playing strategy A (black cells) when it is introduced in a population of individuals playing strategy B (white cells), from the end of the first round to the end of the second round in the case where $b > d$ and $8b > c + 7d$.

each individual is the sum of the payoffs resulting from the interactions with each of the connected neighbours. The update of individuals' strategy is synchronous, i.e. all individuals update their strategy simultaneously in discrete time steps (see Figure 1.2). In stochastic evolutionary dynamics the update of strategies is asynchronous. Randomly selected individuals update their strategy sequentially following some stochastic update rules (but in each generation the number of such updates is equal to the number of individuals occupying the sites of the lattice so that on average every individual updates its strategy once). For example, an individual is chosen at random and updates its strategy adopting the strategy of a random neighbour with a higher payoff with a probability proportional to the difference of their payoffs. Numerous investigations of evolutionary games on different lattices and under different dynamical processes have shown that the results of the evolutionary process might be quantitatively and qualitatively different from the results obtained in the classical evolutionary game theory. For example, although the classical evolutionary game theory predicts that cooperators can never invade defectors in a Prisoner's Dilemma type of game, in the deterministic spatial Prisoner's Dilemma, under some conditions the survival of cooperators is possible and the two strategies can coexist in a dynamic equilibrium (e.g., Nowak and May, 1992; Nowak, 2006). If the evolutionary process is described by a stochastic process, eventually defectors take over the entire population. However, the two strategies might coexist for a very long time

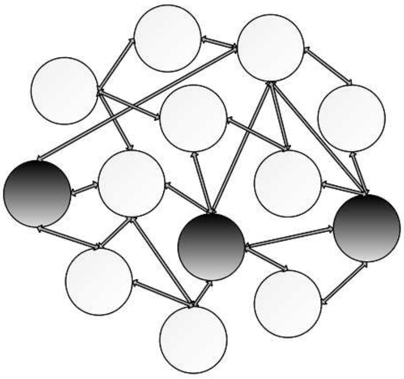


Figure 1.3: A population represented by a graph. Each individual of the population occupies a vertex of the graph. The edges of the graph represent interactions between individuals.

before absorption. Similarly, in the spatial Hawk–Dove game, depending on the update rules and the parameter values, the Hawk strategy might do better or worse than what it does under the assumptions of the classical game theory (e.g., Killingback and Doebeli, 1996; Hauert and Doebeli, 2004).

In real populations, the interactions among individuals usually form more complex connectivity structures. These structures can be represented and modelled as a collection of interacting units. At its simplest, a graph (or network) is a collection of vertices representing well defined units that interact via a set of edges. Lieberman *et al.* (2005) have used tools from graph theory to model evolutionary dynamics in structured populations. The idea was to represent the population of size N by a graph $G(V,E)$, where V is the set of vertices of the graph and E the set of edges. Each of the N individuals of the population occupies a vertex of the graph, and thus $|V| = N$. The edges of the graph represent the interactions between individuals, and thus determine who can replace whom (see Figure 1.3). The structures in the models of spatial games described before are special cases of graphs.

The most widely considered evolutionary process in structured populations represented by graphs is the *invasion process* (IP) (or birth-death process with selection on the birth). The IP is an adaptation of the Moran process on graphs. Initially, a number of mutant individuals X invades a population of resident individuals Y by replacing an equivalent number of Ys at random. Then, at each time-step an individual is randomly selected for reproduction with probability proportional to its fitness. The offspring of that individual, which is a perfect copy of its parent, replaces a neighbouring connected individual which is chosen at random. The probabilities that the offspring of an individual i replaces an individual j, $w_{i,j}$, can be described by the weight matrix $W = [w_{i,j}]$, where $1 \leq i \leq N$, $1 \leq j \leq N$. Obviously, since the offspring of each individual always replaces one other individual, the sum of the elements of each row of the matrix W must be equal to 1, i.e. $\sum_{j=1}^{N} w_{i,j} = 1 \; \forall \; i \in [1,N]$, and thus W is a (right) stochastic matrix. Hence, the matrix W describes the process and since it also represents which vertices are connected to which other vertices, it also determines the graph.

All graphs we study in this work are simple graphs, where each individual occupies exactly one vertex, there are no self-loops, i.e. there is no edge which connects a vertex to itself, and there are no multiple-edges, i.e. every two vertices are connected by at most one edge. In addition, the graphs are undirected, so if we can move from vertex i to vertex j we can also move from vertex j to vertex i, and unweighted. Lastly, all the graphs we consider are connected graphs, i.e. there is a path from any vertex to any other vertex in the graph, and static, i.e. they do not change over time.

On the unweighted complete graph, where every individual is connected to everyone else and the offspring of each individual can replace any other individual with equal probability (so this is a special case of a weighted complete graph where all the weights associated to the edges are equal to $1/(N-1)$), the IP is equivalent to the Moran process. Hence, the fixation probability of $i \in [0,N]$ mutants with relative fitness equal to r on the unweighted complete graph with N vertices is equal to the fixation probability of i mutants in the homogeneous well-mixed population of size N in the Moran process, given by the formula (1.33) for $r \neq 1$ and by i/N for $r = 1$.

Lieberman *et al.* (2005) have proved a theorem, the so-called *isothermal theorem*, which states that in the case of constant fitness, the IP on a graph is equivalent to the Moran process, and thus mutants on that graph have fixation probability equal to that in the Moran process, if and only if the graph is isothermal. An *isothermal graph* is defined to be a graph where the sum of all the weights that lead to every vertex is the same, i.e. the graph where $\sum_{i=1}^{N} w_{i,j}$ is equal to 1 for every $j \in [1,N]$, and thus the matrix W is doubly stochastic (the sum $\sum_{i=1}^{N} w_{i,j}$ for some vertex j is called the *temperature* of vertex j). Such graphs are for example the symmetric graphs where $w_{i,j} = w_{j,i}$ for all i and j (e.g., regular graphs such as spatial lattices and circle graphs, where all the edges have the same weight); but not all isothermal graphs are symmetric.

The isothermal theorem is generalised for a broader class of graphs, where the weights of the edges can be any non-negative real numbers, and thus W is not necessarily stochastic. Consider a process on such a graph, where at each time step the offspring of an individual i replaces an individual j with probability proportional to the weight of the edge $w_{i,j} \in \mathbb{R}_{\geq 0}$ multiplied by the fitness of the individual i. This process is equivalent to the Moran process if and only if the sum of the weights that lead to a vertex is equal to the sum of the weights that leave that vertex, for all the vertices of the graph, i.e. if and only if $\sum_{j=1}^{N} w_{i,j} = \sum_{j=1}^{N} w_{j,i}\ \forall\ i \in [1,N]$. Such graphs which have this property are called *circulation graphs*. The above theorem is called the *circulation theorem*.

Hence, in the case where individuals have constant fitness, there is a large family of graphs, the circulation graphs, that affect neither selection nor random drift, leaving the probability of fixation unaffected. However, as will be shown in Chapter 2, although the fixation probability on circulation graphs is identical to the fixation probability in the Moran process, the mean time to absorption and fixation might be remarkably different.

One question that is raised is the following: are there graphs that amplify or suppress selection and therefore increase or decrease the chance of advantageous mutants to fixate compared to their fixation probability in the Moran process? Furthermore, what happens in the case where the fitness of individuals is not constant but depends on the interaction with their neighbouring individuals, as happens in many natural systems? Lieberman *et al.* (2005) have taken some first significant steps in this direction. They have shown examples of graphs which amplify (suppress) selection over drift, i.e. graphs on which the fixation probability of an advantageous mutant is higher (lower) than its fixation probability in the Moran process (similarly, the fixation probability of a disadvantageous mutant is lower (higher) than its fixation probability in the Moran process). The star graph is an example of such an amplifier graph. The star graph is the graph which has one vertex, the centre, connected to all other vertices, the leaves. It has been shown that in the IP, the fixation probability of a randomly placed mutant with relative fitness r on a very large star of N individuals $(N \to \infty)$ is approached by

$$P_{\text{app}} = \frac{1 - \frac{1}{r^2}}{1 - \frac{1}{r^{2N}}}. \tag{1.38}$$

Hence, the fixation probability of a randomly placed mutant with relative fitness r on a large star graph in the IP is approximately equal to the fixation probability of a mutant with fitness r^2 placed in a homogeneous well-mixed population of the same size in the Moran process. In other words, the star graph amplifies the relative fitness of a mutant individual from r to r^2, i.e selection is enhanced. This is because the probability of mutants to increase their number on the leaves of the star, given a resident in the centre, is r^2 times higher than the respective probability of residents given a mutant in the centre. Thus, the spread of an advantageous mutant ($r > 1$) is favoured on the star while the spread of a disadvantageous mutant is inhibited. There are also graphs in which the amplification (suppression) of the fitness of an advantageous (disadvantageous) mutant can be increased even more than the star graph, and the fixation probability can become arbitrarily closed to 1 (zero) by increasing the number of the vertices in a specific way (e.g., the super-star, the funnel and the metafunnel, see Lieberman *et al.* (2005)). However, on such graphs the mean time required for the system to reach fixation is extremely long. This is demonstrated in Chapters 2 and 3 where the evolutionary process on the star graph is investigated analytically.

In the case where the fitness of individuals depends on the interactions with neighbouring individuals, and thus on the composition of the population, the evolutionary process is more sensitive to the graph structure. As is demonstrated in Chapter 2, in this case, even on circulation graphs the fixation probability might be significantly varied.

Based on Lieberman *et al.* (2005), a large amount of interesting studies have followed giving insight into the effect of the population structure on various evolutionary processes (e.g., Ohtsuki *et al.* (2006); Ohtsuki and Nowak (2006a,b); Santos *et al.* (2006b); Ohtsuki *et al.* (2007a,b); Taylor *et al.* (2007); Broom and Rychtář (2008); Ohtsuki and Nowak (2008); Tarnita *et al.* (2009); Broom *et al.* (2010a); Hadjichrysanthou *et al.* (2011); van Veelen and Nowak (2012). See also Nowak *et al.* (2010) and Shakarian *et al.* (2012) for reviews).

1.6 Models of kleptoparasitism

Game theory has facilitated the mathematical modelling of systems emanated from natural and social sciences. In this work, based on the modelling framework provided by game theory, we model and study a very common foraging behaviour of animals, kleptoparasitism.

Kleptoparasitism is a form of feeding, where animals attempt to steal food already discovered by others. Different forms of kleptoparasitic behaviour are observed in many species in the animal kingdom, for example species of spiders (e.g., Coyle *et al.*, 1991), birds (e.g., Brockmann and Barnard, 1979), snails (e.g., Iyengar, 2002), lizards (e.g., Cooper and Pérez-Mellado, 2003), fish (e.g., Hamilton and Dill, 2003), primates (e.g., Janson, 1985), carnivores (e.g., Carbone *et al.*, 2005) and insects (e.g., Erlandsson, 1988). This behaviour of animals has been well documented in a review paper (Iyengar, 2008). The biological phenomenon of kleptoparasitism has attracted the interest of many researchers from different areas. There are a number of theoretical models focused on the kleptoparasitic behaviour of animals using different mathematical methods, in particular evolutionary game theory. Two of the fundamental game-theoretical models that consider kleptoparasitic behaviour are the producer-scrounger model, originally introduced by Barnard and Sibly (1981), and the model of Broom and Ruxton (1998).

In its original form, the producer-scrounger game is a frequency-dependent game where animals forage for food using two strategies. They either search for food (producer's strategy) or search for opportunities to kleptoparasitise (scrounger's strategy). The scrounger strategy does better when scroungers are rare and worse when they are common. When the frequency of the two strategies is such that the payoff obtained by each strategy is the same, there is a stable equilibrium where the two strategies coexist. Many variations of this model have followed in order to consider different factors that might affect the foraging process (e.g., Caraco and Giraldeau, 1991; Vickery *et al*., 1991; Dubois and Giraldeau, 2005). One key feature of this type of model is that food is usually discovered in patches and can be easily split between foraging animals. Hence, the concept of food sharing is central to these models. In addition, in these models costs from aggressive strategies are energetic, rather than time, costs. Thus, the different strategies do not directly affect the distribution of feeding and foraging animals, and the main effect of population density is to reduce the "finder's share", the portion of the food eaten by a finder before other foragers discover it.

The model of Broom and Ruxton (1998), based on the mechanistic model of Ruxton and Moody (1997), follows a different approach. Using a game-theoretical approach, the authors have considered the ecological conditions under which attacking to steal the food from other animals when the opportunity arises is the best strategy that foraging animals should adopt in order to maximise their food intake rate and consequently their fitness. Food in this model comes in single indivisible items, which must be consumed completely by an individual. Thus, food can never be shared and challenging animals attempt to steal the whole item from the owner, or not. Note that the population density has a direct effect in this model as fights take time; this loss of time is the cost to more aggressive strategies, and thus the more potential kleptoparasites there are, the more time is wasted on fighting. The present research work studies the evolution of kleptoparasitic populations under different circumstances based on the model of Broom and Ruxton (1998). Thus, let us discuss this model in more detail.

According to this model, each of the animals in a population of foragers either searches for food, has already acquired and is handling a food item prior to its consumption, or fights with another animal over a food item. Let us denote by P the population density, by S the density of searchers, by H the density of handlers and

Table 1.1: Notation of the basic game-theoretical model of kleptoparasitism of Broom and Ruxton (1998)

Population's densities	**Meaning**
P	Density of the population
S, H, F	Density of searchers, handlers and fighters
Model Parameters	**Meaning**
$v_f f$	Rate at which foragers find undiscovered food
$v_h H$	Rate at which foragers encounter handlers
t_h	Expected time for a handler to consume a food item if it is not attacked
$t_a/2$	Expected duration of a fight
α	The probability that the attacker wins the fight
Strategies	**Meaning**
p	The probability that a searcher attacks a handler when they meet

by F the density of animals which are involved in a fight over a food item. When a foraging animal encounters an animal in the handling state, it can either decide with probability p to attack in order to steal the prey, or with probability $1 - p$ to ignore the handler animal and continue searching. There is a constant density of food items f available and searchers cover an area v_f per unit time whilst searching for food, so animals find food at rate $v_f f$. The unit of time can vary depending on the animal species, but this is usually the second or the minute (see for example, Hockey *et al.*, 1989). If a handler animal is not attacked, it consumes its food item in a time drawn randomly from an exponential distribution with mean t_h. Attacked animals always defend their food and a fight takes place. Searchers encounter handlers and engage in a fight at rate pv_hH. A fight lasts for a time drawn randomly from an exponential distribution with mean $t_a/2$. At the end of the fight, each of the two animals wins the food with equal probability, i.e. with probability 0.5. The loser returns to the searching state while the winner starts handling the food item. The model notation is summarised in Table 1.1.

The system of equations constructed to describe the dynamics of the three sub-populations is the following:

$$\frac{dS}{dt} = \frac{1}{t_h}H + \frac{1}{t_a}F - v_f fS - pv_hSH, \tag{1.39}$$

$$\frac{dH}{dt} = v_f fS + \frac{1}{t_a}F - \frac{1}{t_h}H - pv_hSH, \tag{1.40}$$

$$\frac{dF}{dt} = 2pv_hSH - \frac{2}{t_a}F. \tag{1.41}$$

Broom and Ruxton (1998) considered the optimal value of p to be the value which minimises the mean time required for a searcher that has just encountered a handler to start handling a food item, as the less the required time, the higher the food intake rate.

The food intake rate, γ, is given by

$$\gamma = \frac{H}{t_h P}, \tag{1.42}$$

where H is the proportion of handlers in the equilibrium state and is given by

$$H = \frac{-(t_h \nu_f f + 1) + \sqrt{(t_h \nu_f f + 1)^2 + 4pt_h t_a \nu_f f \nu_h P}}{2pt_a \nu_h}. \tag{1.43}$$

It has been shown that there is always a unique ESS that animals can use. For every set of parameter values, the intake rate of a searcher is maximised when it either challenges a handler at every opportunity, or it always ignores a handler and continues searching for another food item for itself. It is proved that the optimal strategy that should be adopted depends only on the fight duration, $t_a/2$, and the rate at which a food item is discovered, $\nu_f f$. In particular, it is shown that when $t_a \nu_f f > 1$, i.e. when food can be discovered within a short time or/and any aggressive interactions have a high time cost, a searcher animal should never attempt to steal a food item from a handler. Hence, under these conditions the optimal strategy is $p = 0$. On the other hand, if $t_a \nu_f f < 1$, i.e. the fight time cost is low or/and the available food is scarce, then searchers should attempt to steal the food from another animal at every opportunity, i.e. the optimal strategy is $p = 1$. In the case where $t_a \nu_f f = 1$, the choice of the strategy of the searcher is irrelevant.

Despite the simplicity of the model of Broom and Ruxton (1998), interesting predictions are made about the ecological conditions under which animals should attempt to steal food from other animals. However, this model is based on various assumptions. One of the main assumptions is that the only choice for a handler animal when it is challenged is to defend its food, and thus in this case a fight always takes place. In addition, it is assumed that animals involved in an aggressive interaction are equally likely to win the fight and obtain the food. Broom *et al.* (2004), in order to relax these assumptions, have later reconstructed the model of Broom and Ruxton (1998) in a more general and realistic framework. In this model, an attacked animal has, apart from the possibility to defend its food, the possibility to surrender its food to the attacker and resume searching for another food item, avoiding the time cost of a fight. In addition, different competitive abilities between the attacker and the attacked animal are introduced, i.e. the probability of the attacking animal winning and obtaining the food, α, varies between 0 and 1, as happens in natural situations. In general, the circumstances under which fights occur might give a high advantage to defender or attacker (the attacker might have to catch the defender in the air, but the defender may be hampered by a heavy food item) and so this probability may be significantly less or greater than 0.5. In this extended model, it has been shown that there are three possible ESSs; the Hawk strategy where animals challenge handlers at every opportunity and defend their food when challenged, the Marauder strategy where animals always attempt to steal the food from other animals but never defend their food when attacked, and the Retaliator strategy where animals never attack other animals to steal their food, but always resist and defend their food when attacked. In contrast to the original model of Broom and Ruxton (1998), where for every set of parameter values there is always a unique ESS, in the extended model there are cases where between two regions in parameter space in each of which there is a unique ESS, there might be a region where the two ESSs are possible to exist simultaneously. In the case where each of the two animals which are engaged in a fight are equally likely to win and obtain the food, i.e. $\alpha = 0.5$ (this is a main assumption of the model of Broom and Ruxton (1998)), the Retaliator strategy is never an ESS and depending on the ecological parameters either the Hawk or the Marauder strategy is the unique ESS or both are ESSs together. In particular, it is shown that increasing $\nu_f f$, i.e. increasing the rate at which food items are discovered, or increasing the fight duration $t_a/2$, discourages any aggressive interactions over food making the Marauder strategy the optimal strategy. Note that in this case the occurrence of the Hawk strategy as an ESS is independent of the parameters P, ν_h and t_h. However, the variation of these parameters affects the occurrence of the Marauder strategy as an ESS. For example, the decrease of $\nu_h P$ or the decrease of t_h make this strategy less attractive. In the general case where the attacker and the attacked animal do not have as equal probability to win the fight ($\alpha \neq 0.5$), it has been shown that when $t_a/2$ and α are high, then the defence of a food item is not favoured, whilst attacking handlers that surrender their food without a fight are favoured. In particular, when $t_a/2$ is very high, the Marauder strategy is the only ESS. This also occurs when α is very high, given that $t_a/2$ is not very small. As one could expect, when $t_a/2$ is small and the probability that a handler defends its food successfully, $1-\alpha$, is high then the Retaliator strategy is favoured. Note that the Retaliator strategy is an ESS only when handlers have probability of at least 0.5 to win the fight, otherwise this strategy is invaded by attacking strategies. When $t_a/2$ is small and the probability of defending a food item successfully is neither very high nor very small, the Hawk strategy might be an ESS. The other parameters, P, $\nu_f f$, ν_h and t_h, are also very important for the strategic choices of animals. For example, as we have seen in the case where each of the contestants has an equal probability to win, the increase of $\nu_f f$ favours the Marauder strategy.

A series of publications has appeared developing the original model of Broom and Ruxton (1998) in a number of ways (e.g., Broom and Ruxton, 2003; Broom and Rychtář, 2007; Luther *et al.*, 2007; Yates and Broom, 2007; Broom *et al.*, 2008; Broom and Rychtář, 2009, 2011). Crowe *et al.* (2009) provide a brief review on the main theoretical work on kleproparasitism prior to the investigation of a stochastic model of kleptoparasitism in finite populations. A comparison between some main models of kleptoparasitism is discussed in Vahl (2006) and an alternative model is presented. There is also a series of related mechanistic, but not game-theoretic, models which investigate interference competition where foraging animals engage in aggressive interactions in order for example to defend their territory, resulting in negative effects on their foraging efficiency (e.g., Beddington, 1975; Ruxton *et al.*, 1992; van der Meer and Ens, 1997; Vahl, 2006; Smallegange and van der Meer, 2009; van der Meer and Smallegange, 2009).

1.7 Contributions

In this work, we have considered analytically the evolutionary game dynamics in populations represented by a complete graph, a circle and a star graph. Although there have been numerous studies carried out for the investigation of the influence of the population structure on the evolution of populations, in most of these the results have been derived under strong assumptions, for example under the assumption that the population size is very large, or they are based on approximation models and numerical simulations. We have derived the exact solutions of some of the most important quantities in a stochastic evolutionary process. These include the fixation probability and the speed of the evolutionary process under different conditions, starting from any initial composition of a population consisting of two types of individuals (see Chapters 2 and 3). Especially, the formulae of the mean time to absorption and fixation on the star graph are the first general formulae for absorption and fixation times derived on an irregular graph. These solutions give the possibility of a detailed consideration of the evolutionary process in different cases, for example for different population sizes, different games and so on. In previous studies a great emphasis has been given to the fixation probability and the study of the speed of the evolutionary process is relatively rare. However, this quantity is also very important, especially in cases where evolution favours the existence of a mixed population. In such cases, the fixation probability might not be sufficient to describe the evolutionary dynamics of the system. For example, as we will see in Chapters 2 and 3, although a star graph favours the fixation of an advantageous mutant with respect to its fixation probability, the time needed for its fixation might be extremely long. A big part of this work has been published as two separate research articles in *Proceedings of the Royal Society A*. These are the articles Broom *et al*. (2010a) and Broom *et al*. (2010b).

A step forward in the research on the influence of the structure of the population on the evolutionary process is the investigation of the process under different strategy update rules. In this work, through an analytic approach it is shown that the choice of the update rules might be crucial when the population has a non-homogeneous structure (see Chapter 3). This work has been published as a research article in *Dynamic Games and Applications*. This is the article Hadjichrysanthou *et al*. (2011).

The possibilities of an analytic investigation of the evolutionary dynamics on graphs are very limited and the resort to numerical and approximation methods is necessary for the exploration of the dynamics in complex graphs. This work (see Chapter 4) proposes an effective approximation method for the study of the evolution of structured resident populations when invaded by mutant types of individuals. This is a very promising method that can be applied to a wide range of graphs and can significantly contribute to the consideration of the characteristics of the graphs that affect the evolution of populations in different scenarios. This work has been published as a research article in the *Journal of Theoretical Biology*. This is the article Hadjichrysanthou *et al*. (2012).

A basic game-theoretical model of kleptoparasitism has been considered in the case where the population of foraging animals forms a non-homogeneous structure (see Chapter 5). This relaxes some of the strong implicit assumptions of some classic models, such as the homogeneously mixing of animals and the infiniteness of the population size. Although the steps taken in this direction are few, this work sets the foundations for the study of some classic evolutionary models of foraging behaviour of animals in a more realistic framework.

Cooperative and food sharing behaviour has been observed in a wide variety of animals and has attracted the research interest of scientists from different fields. Many mathematical models have been constructed in order to explore the reasons why animals share their food. However, many of these models were not sufficient to explain why in many situations animals present this behaviour. In this work, based on some classic models of kleptoparasitism, we have constructed a game-theoretical model for the examination of food sharing behaviour of animals in kleptoparasitic populations (see Chapter 6). Although this work is based on a number of assumptions, it gives some important answers and raises some research questions for further study on understanding this interesting animal behaviour. This work has been published as a research article in *Behavioral Ecology*. This is the article Hadjichrysanthou and Broom (2012).

1.8 Outline

In Chapter 2, we investigate analytically the evolutionary game dynamics on the complete graph, the circle and the star graph. We derive the exact formulae for the fixation probability and the speed of the evolutionary process under different conditions. These formulae can be applied to stochastic processes where there is no mutation and the size of each type of individuals in each time step can vary at most by one. We apply the results derived following the rules of the IP. Through numerical examples we compare the impact of the three structures on the above quantities. We do this comparison in two specific cases. Firstly, we examine the case where individuals have constant fitness. Then, we study the case where the fitness is not constant but depends on the composition of the population. The widely used Hawk–Dove game is considered as an example.

In Chapter 3, we investigate the evolutionary dynamics under three important update rules additional to the IP and we explore the influence of the change of the update rule on the evolutionary process when the population has a non-homogeneous structure. We study analytically an evolutionary game between two strategies interacting on the extreme heterogeneous star graph. The evolutionary process is considered in different scenarios: the constant fitness case and the frequency dependent fitness case when the individuals of the population play a Hawk–Dove game, a Prisoner’s Dilemma and a coordination game.

In Chapter 4, we propose an approximation method to model evolutionary game dynamics on complex graphs. Comparisons of the predictions of the model constructed with the results of computer simulations reveal the effectiveness of the method and the improved accuracy that it provides when, for example, compared to well-known pair approximation methods. As an example, we investigate how the Hawk and Dove strategies in a Hawk–Dove game spread in a population represented by a random regular graph, a random graph and a scale-free network, and we examine the features of the graph which affect the evolution of the population when individuals play this particular game.

Chapter 5 discusses a simple model of the evolution of kleptoparasitic populations in the case where the animal population has a structure represented by a graph. Using the pair approximation method as well as through stochastic simulations we explore the evolution of the population when it is represented by a regular graph, a random graph and a scale-free network, and consider the characteristics of the graph that might influence the evolution of such populations.

In Chapter 6, we propose a game-theoretical model for the exploration of those ecological conditions that favour food sharing among animals in kleptoparasitic populations. Analysis of the model shows that food sharing should occur in a wide range of ecological conditions. In particular, if food availability is limited, the sharing process does not greatly reduce the short-term consumption rate of food, and food defense has a high cost and/or a low probability of success, then the use of the food sharing strategy is beneficial.

In Chapter 7, we summarise the main conclusions and contributions of this work and we discuss some research topics of future interest.

CHAPTER 2

Evolutionary dynamics on simple graphs

2.1 Introduction

In this chapter, we study analytically the stochastic evolutionary game dynamics of finite populations represented by three simple graphs; the complete graph, the circle and the star graph. We consider the evolution of populations playing a strategy B when invaded by a number of mutant individuals that play a different strategy, a strategy A. The game played is described by the payoff matrix (1.2).

The complete graph (see Figure 2.1a) is the graph where every individual is connected to every other individual. This graph is the regular graph with the highest degree, equal to $N-1$, where N is the population size. The homogeneous well-mixed population is a special case of a complete graph where all edges have identical weights.

The circle (see Figure 2.1b) is a graph where each vertex is connected to two other vertices. It is the regular graph with the smallest degree, equal to 2. The circle is a graph which has been widely used in different fields. The evolutionary process on the cycle has been investigated in various scenarios (e.g., Lieberman *et al*., 2005; Nowak, 2006; Ohtsuki and Nowak, 2006a; Ohtsuki *et al*., 2006; Grafen, 2007; Masuda, 2009; Tarnita *et al*., 2009; Broom *et al*., 2010a; van Veelen and Nowak, 2012).

The star graph (see Figure 2.1c) is an irregular graph where n vertices, the leaves, are connected to only one vertex, the centre. Thus, the star has average degree equal to $2n/(n+1)$. For very large population size this approaches the degree of the circle. However, as we will see later, the evolutionary process on the two graphs is remarkably different. Evolution on a star-structured population has been commonly studied (e.g., Lieberman *et al*., 2005; Nowak, 2006; Broom and Rychtář, 2008; Fu *et*

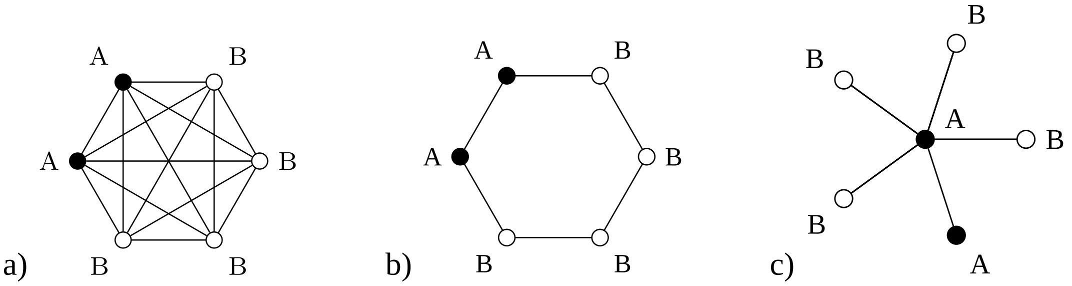


Figure 2.1: Structured populations represented by graphs with $N = 6$ vertices, two of which are occupied by individuals playing strategy A (black vertices) while the rest of the vertices are occupied by individuals playing strategy B (white vertices). (a) A complete graph, (b) a circle graph, and (c) a star graph. The center vertex of the star and one of the $n = 5$ leaves ($i = 1$) are the vertices occupied by individuals playing strategy A.

al., 2009; Masuda, 2009; Tarnita *et al.*, 2009; Broom *et al.*, 2010a). As we have seen in Section 1.5, the fixation probability of a single mutant individual with relative fitness r introduced into a resident population structured as a star was first considered in Lieberman *et al.* (2005) following the rules of the invasion process (IP) and assuming a large population size. An exact formula of the fixation probability in this case was given later in Broom and Rychtář (2008) (see also Masuda, 2009). This has been extended in Broom *et al.* (2010a) to the more complicated case of frequency dependent fitness by applying evolutionary game theory. In the same paper, the absorption and fixation time of a mutant under the IP have also been considered. In Broom *et al.* (2009), it is shown through a numerical investigation that at least for small graphs, under the IP the star is the structure in which a randomly placed mutant has the highest chance of fixation.

The graph structures we study are all commonly considered structures in part due to their symmetry and lack of complexity. In general, the analytic investigation of the evolutionary process in structured populations is very limited mainly due to the large number of complex equations that one has to solve. The number of equations corresponds to the number of distinct states on the graph (mutant-resident formations) that the system can reach. For an arbitrary graph of N vertices, since every vertex can be occupied by either a resident or a mutant individual, there are 2^N possible states that the system can reach. However, in many graphs many of these states are identical, in the sense that one state can be obtained from the other due to symmetries of the graph, and thus the system of equations can be significantly reduced. For example, on a complete graph only $N+1$ of the 2^N possible states are distinct. The number of the distinct states is the same on the circle given that mutant individuals always form a connected segment, otherwise this number is much larger. On the star the number is larger, equal to $2N$. Broom and Rychtář (2008) (see also

Broom *et al.*, 2010b) using graph automorphisms have calculated the total number of the distinct states on an arbitrary graph, and thus demonstrated the large number of equations in the system and the complexity of analytic investigations.

In Sections 2.2 and 2.3, we derive the exact solutions of the fixation probability and the mean absorption and fixation time starting from any number of A individuals placed on a complete graph, a circle (as a segment) and a star graph. The solutions are general and can be applied to stochastic evolutionary processes where there is no mutation, just selection, and in each time step the number of mutants increases by one, decreases by one or remains the same. In Section 2.4, we apply our results to the widely used IP. In section 2.5, we find appropriate conditions under which one strategy is favoured over the other on each of the graphs. Then, in Section 2.6, through numerical examples we compare the impact of the population size and the individuals' fitness on the quantities we consider, on the three graphs under the rules of the IP. We note that the solutions of the mean time to absorption and the mean fixation time of mutants in this process have the same behaviour as the individuals' fitness and the population size vary. However, when mutant individuals become extinct it usually happens in a short time, so the number of time-steps needed for mutants' fixation in each case is higher; in this work we will mainly focus on the mean time to absorption.

2.2 Evolutionary games on the complete graph and the circle

Since the uniformly weighted (or unweighted) complete graph is identical to a homogeneous well-mixed population, the fixation probability, the mean time to absorption and the mean fixation time starting from $i \in [1, N]$ individuals playing strategy A is given by the formulae (1.27), (1.34) and (1.35), respectively.

On the circle, the spread of a single A individual (or a number of A individuals placed initially on connected vertices) always leads to a connected segment of As. This obviously holds only in processes where there is no mutation, otherwise the segments of As and Bs could split by the replacement of an A individual by a B individual which is the offspring of a neighbouring A, or vice versa. Thus, any transition from one state to a different state happens only when an individual in the boundaries of the two connected segments (one consisting of As and one of Bs) is replaced by the offspring of a neighbour of different type. As on a complete graph, on a circle any two formations of i As and $N-i$ Bs are equivalent. Thus, the fixation probability and the mean time to absorption and fixation starting from any number of individuals playing strategy A on a circle graph (given that these are connected) are also given by the formulae (1.27), (1.34) and (1.35), respectively.

2.3 Evolutionary games on the star graph

In this section, we consider analytically and find exact formulae for the fixation probability, the absorption and fixation time, and the mean number of transitions before absorption and fixation occur, starting from any number of A individuals placed at any possible position on a star of any size. As above, we assume that in the evolutionary process there is no mutation.

Let $p_{i,j}^{XY}$ denote the transition probability from a state with i A individuals on the leaves and an X$\in \{A,B\}$ individual in the center to the state with j A individuals on the leaves and a Y$\in \{A,B\}$ individual in the center. Since in the process there is no mutation and the number of A individuals can increase or decrease at most by one, only $p_{i,i+1}^{AA}$, $p_{i,i}^{AB}$ and $p_{i,i}^{AA} = 1 - p_{i,i+1}^{AA} - p_{i,i}^{AB}$ $(0 \leq i \leq n-1)$, and $p_{i,i-1}^{BB}$, $p_{i,i}^{BA}$ and $p_{i,i}^{BB} = 1 - p_{i,i-1}^{BB} - p_{i,i}^{BA}$ $(1 \leq i \leq n)$ can be non-zero.

2.3.1 Fixation probability on the star graph

Consider a star graph with n leaves being at the state where an X individual is in the centre, and i X individuals and $n-i$ Y individuals, $0 \leq i \leq n-1$, are on the leaves. In the next time step, the number of X individuals on the leaves can increase by one, the number of X individuals on the leaves can remain the same but the individual in the centre be replaced by the offspring of a Y individual on the leaves, or the system can remain at the same state because of a replacement of either the X individual in the centre by the offspring of an X individual on the leaves, or a replacement of an X individual on the leaves by the offspring of the central individual.

Let us denote by ${}^{X}P_i^A$ $\left({}^{X}P_i^B\right)$ the probability that individuals playing strategy X fixate in a population originally consisting of i A individuals on the leaves and an A (a B) individual in the centre.

The fixation probabilities ${}^{A}P_i^A$ and ${}^{A}P_i^B$ are given by the solutions of the following system of equations

$$ {}^{A}P_i^A = p_{i,i+1}^{AA}\,{}^{A}P_{i+1}^A + p_{i,i}^{AB}\,{}^{A}P_i^B + \left(1 - p_{i,i+1}^{AA} - p_{i,i}^{AB}\right){}^{A}P_i^A, \quad 0 \leq i \leq n-1, \tag{2.1} $$

$$ {}^{A}P_i^B = p_{i,i}^{BA}\,{}^{A}P_i^A + p_{i,i-1}^{BB}\,{}^{A}P_{i-1}^B + \left(1 - p_{i,i}^{BA} - p_{i,i-1}^{BB}\right){}^{A}P_i^B, \quad 1 \leq i \leq n, \tag{2.2} $$

with conditions on the absorbing states

$$ {}^{A}P_{0}^{B} = 0, \tag{2.3} $$

$$ {}^{A}P_{n}^{A} = 1. \tag{2.4} $$

Rearranging equations (2.1)–(2.2) yields

$$ {}^{A}P_{i}^{A} = \pi_{i,i+1}^{AA}\,{}^{A}P_{i+1}^{A} + \pi_{i,i}^{AB}\,{}^{A}P_{i}^{B}, \quad 0 \le i \le n-1, \tag{2.5} $$

$$ {}^{A}P_{i}^{B} = \pi_{i,i}^{BA}\,{}^{A}P_{i}^{A} + \pi_{i,i-1}^{BB}\,{}^{A}P_{i-1}^{B}, \quad 1 \le i \le n, \tag{2.6} $$

where π denotes the transition probability conditional on the system not remaining in the same state, i.e.

$$ \pi_{i,i+1}^{AA} = 1 - \pi_{i,i}^{AB} = \frac{p_{i,i+1}^{AA}}{p_{i,i+1}^{AA} + p_{i,i}^{AB}}, \quad 0 \le i \le n-1, \tag{2.7} $$

$$ \pi_{i,i}^{BA} = 1 - \pi_{i,i-1}^{BB} = \frac{p_{i,i}^{BA}}{p_{i,i}^{BA} + p_{i,i-1}^{BB}}, \quad 1 \le i \le n. \tag{2.8} $$

Equation (2.5) can be written as

$$ {}^{A}P_{i}^{A} = \frac{1}{\pi_{i-1,i}^{AA}}\,{}^{A}P_{i-1}^{A} - \frac{\pi_{i-1,i-1}^{AB}}{\pi_{i-1,i}^{AA}}\,{}^{A}P_{i-1}^{B}, \quad 1 \le i \le n-1. \tag{2.9} $$

From equation (2.6) and (2.3), for $i = 1$ we get

$$ {}^{A}P_{1}^{B} = \pi_{1,1}^{BA}\,{}^{A}P_{1}^{A}. \tag{2.10} $$

From (2.9), for $i = 2$ we get

$$ {}^{A}P_{2}^{A} = \frac{1}{\pi_{1,2}^{AA}}\,{}^{A}P_{1}^{A} - \frac{\pi_{1,1}^{AB}}{\pi_{1,2}^{AA}}\,{}^{A}P_{1}^{B} \overset{(2.10)}{=} \left(\frac{1 - \pi_{1,1}^{AB}\pi_{1,1}^{BA}}{\pi_{1,2}^{AA}} \right) {}^{A}P_{1}^{A}. \tag{2.11} $$

But, $\pi_{1,1}^{BA} = 1 - \pi_{1,0}^{BB}$ and $\pi_{1,2}^{AA} = 1 - \pi_{1,1}^{AB}$. Thus, from (2.11) we obtain

$$ {}^{A}P_{2}^{A} = \left(1 + \frac{\pi_{1,1}^{AB}\pi_{1,0}^{BB}}{\pi_{1,2}^{AA}} \right) {}^{A}P_{1}^{A}. \tag{2.12} $$

From (2.6), for $i = 2$, using (2.10) and (2.12) we get

$$ {}^{A}P_{2}^{B} = \left(\pi_{2,2}^{BA} + \pi_{1,1}^{BA}\pi_{2,1}^{BB} + \frac{\pi_{1,1}^{AB} + \pi_{1,0}^{BB}\pi_{2,2}^{BA}}{\pi_{1,2}^{AA}} \right) {}^{A}P_{1}^{A}. \tag{2.13} $$

From (2.9), for $i = 3$, using (2.12)–(2.13) we get

$$
{}^{A}P_3^A = \left(\frac{1}{\pi_{2,3}^{AA}} + \frac{\pi_{1,1}^{AB}\pi_{1,0}^{BB}}{\pi_{1,2}^{AA}\pi_{2,3}^{AA}} - \frac{\pi_{2,2}^{AB}\pi_{2,2}^{BA}}{\pi_{2,3}^{AA}} - \frac{\pi_{1,1}^{BA}\pi_{2,2}^{AB}\pi_{2,1}^{BB}}{\pi_{2,3}^{AA}} - \frac{\pi_{1,1}^{AB}\pi_{1,0}^{BB}\pi_{2,2}^{AB}\pi_{2,2}^{BA}}{\pi_{1,2}^{AA}\pi_{2,3}^{AA}} \right) {}^{A}P_1^A. \tag{2.14}
$$

Using that $\pi_{1,1}^{BA} = 1 - \pi_{1,0}^{BB}$, $\pi_{1,2}^{AA} = 1 - \pi_{1,1}^{AB}$, $\pi_{2,2}^{AB} = 1 - \pi_{2,3}^{AA}$ and $\pi_{2,2}^{BA} = 1 - \pi_{2,1}^{BB}$, from (2.14), after some calculations we obtain

$$
{}^{A}P_3^A = \left(1 + \frac{\pi_{1,1}^{AB}\pi_{1,0}^{BB}}{\pi_{1,2}^{AA}} + \frac{\pi_{2,2}^{AB}\pi_{2,1}^{BB}\pi_{1,0}^{BB}}{\pi_{1,2}^{AA}\pi_{2,3}^{AA}} \right) {}^{A}P_1^A. \tag{2.15}
$$

Continuing in the same way, we find that

$$
{}^{A}P_i^A = D(1,i)\,{}^{A}P_1^A, \quad 1 \leq i \leq n, \tag{2.16}
$$

where

$$
D(l,m) = 1 + \sum_{j=l}^{m-1} \pi_{j,j}^{AB} \prod_{k=l}^{j} \frac{\pi_{k,k-1}^{BB}}{\pi_{k,k+1}^{AA}}. \tag{2.17}
$$

From (2.16) and (2.4) we obtain

$$
{}^{A}P_1^A = \frac{1}{D(1,n)}. \tag{2.18}
$$

Therefore, substituting (2.18) into (2.16) we find that ${}^{A}P_i^A$ $(1 \leq i \leq n)$ is given by

$$
{}^{A}P_i^A = \frac{D(1,i)}{D(1,n)}, \quad 1 \leq i \leq n. \tag{2.19}
$$

From equation (2.6) and (2.3) we find

$$
{}^{A}P_i^B = \sum_{j=1}^{i} \pi_{j,j}^{BA}\, {}^{A}P_j^A \prod_{k=j+1}^{i} \pi_{k,k-1}^{BB}, \quad 1 \leq i \leq n. \tag{2.20}
$$

From (2.5) and (2.3) we get that for $i = 0$,

$$
{}^{A}P_0^A = \pi_{0,1}^{AA}\, {}^{A}P_1^A = \frac{\pi_{0,1}^{AA}}{D(1,n)}, \tag{2.21}
$$

and from (2.20) we get that for $i = 1$,

$$
{}^{A}P_1^B = \pi_{1,1}^{BA}\, {}^{A}P_1^A = \frac{\pi_{1,1}^{BA}}{D(1,n)}. \tag{2.22}
$$

The average fixation probability of a single A individual randomly placed on the star, ${}^{A}P$, is given by

$$ {}^{A}P = \frac{1}{n+1}\,{}^{A}P_0^A + \frac{n}{n+1}\,{}^{A}P_1^B = \frac{n\pi_{1,1}^{BA} + \pi_{0,1}^{AA}}{n+1}\frac{1}{D(1,n)}. \tag{2.23} $$

(see also Tarnita *et al.* (2009) for an alternative formula for the fixation probability of a single mutant on the star).

2.3.2 Mean time to absorption on the star graph

As before, starting from a state with an X individual in the centre and i X individuals and $n-i$ Y individuals on the leaves, $0 \le i \le n-1$, in one time step (this corresponds to the addition of 1 in the equations (2.24) and (2.25) below) we might have a replacement of a Y individual on the leaves by the offspring of the X individual in the centre, a replacement of the X individual in the centre by the offspring of a Y individual on the leaves, or a replacement of an individual X by an individual of the same type.

Let us denote by T_i^A $\left(T_i^B\right)$ the mean time to absorption starting from i A individuals on the leaves and an A (a B) in the centre. T_i^A and T_i^B are the solutions of the system

$$ T_i^A = p_{i,i+1}^{AA}T_{i+1}^A + p_{i,i}^{AB}T_i^B + \left(1 - p_{i,i+1}^{AA} - p_{i,i}^{AB}\right)T_i^A + 1, \quad 0 \le i \le n-1, \tag{2.24} $$

$$ T_i^B = p_{i,i}^{BA}T_i^A + p_{i,i-1}^{BB}T_{i-1}^B + \left(1 - p_{i,i}^{BA} - p_{i,i-1}^{BB}\right)T_i^B + 1, \quad 1 \le i \le n, \tag{2.25} $$

$$ T_0^B = 0, \tag{2.26} $$

$$ T_n^A = 0. \tag{2.27} $$

Rearranging equations (2.24)–(2.25) we obtain the following system

$$ T_i^A = \pi_{i,i+1}^{AA}T_{i+1}^A + \pi_{i,i}^{AB}T_i^B + \frac{1}{p_{i,i+1}^{AA} + p_{i,i}^{AB}}, \quad 0 \le i \le n-1, \tag{2.28} $$

$$ T_i^B = \pi_{i,i}^{BA}T_i^A + \pi_{i,i-1}^{BB}T_{i-1}^B + \frac{1}{p_{i,i-1}^{BB} + p_{i,i}^{BA}}, \quad 1 \le i \le n. \tag{2.29} $$

Equation (2.28) can be written in the following form

$$ T_i^A = \frac{1}{\pi_{i-1,i}^{AA}}T_{i-1}^A - \frac{\pi_{i-1,i-1}^{AB}}{\pi_{i-1,i}^{AA}}T_{i-1}^B - \frac{1}{\pi_{i-1,i}^{AA}\left(p_{i-1,i}^{AA} + p_{i-1,i-1}^{AB}\right)}, \quad 1 \le i \le n-1. \tag{2.30} $$

Solving the system of equations (2.29)–(2.30) and (2.26)–(2.27) inductively, as before, we find

$$T_i^A = D(1,i)T_1^A - \sum_{l=2}^{i} D(l,i)E(l), \quad 1 \le i \le n, \tag{2.31}$$

where

$$E(l) = \frac{\pi^{AB}_{l-1,l-1}}{\pi^{AA}_{l-1,l}} \sum_{j=1}^{l-1} \left(\frac{\prod_{k=j+1}^{l-1} \pi^{BB}_{k,k-1}}{p^{BB}_{j,j-1} + p^{BA}_{j,j}} \right) + \frac{1}{p^{AA}_{l-1,l}}. \tag{2.32}$$

For $i = n$, $T_n^A = 0$. Hence, from (2.31) we get

$$T_1^A = \frac{1}{D(1,n)} \sum_{l=2}^{n} D(l,n)E(l). \tag{2.33}$$

Substituting (2.33) into (2.31) and using (2.19) we find that T_i^A $(1 \le i \le n)$ is given by

$$T_i^A = {}^A P_i^A \sum_{l=2}^{n} D(l,n)E(l) - \sum_{l=2}^{i} D(l,i)E(l), \quad 1 \le i \le n. \tag{2.34}$$

From equation (2.29) and (2.26) we find

$$T_i^B = \sum_{j=1}^{i} \pi^{BA}_{j,j} \left(T_j^A + \frac{1}{p^{BA}_{j,j}} \right) \prod_{k=j+1}^{i} \pi^{BB}_{k,k-1}, \quad 1 \le i \le n. \tag{2.35}$$

From (2.28) and (2.26) we have that for $i = 0$,

$$T_0^A = \pi^{AA}_{0,1} T_1^A + 1 = \frac{\pi^{AA}_{0,1}}{D(1,n)} \sum_{l=2}^{n} D(l,n)E(l) + 1, \tag{2.36}$$

where we have used that $p^{AA}_{0,1} + p^{AB}_{0,0} = 1$.
From (2.35) we have that for $i = 1$,

$$T_1^B = \pi^{BA}_{1,1} T_1^A + \frac{1}{p^{BB}_{1,0} + p^{BA}_{1,1}} = \frac{\pi^{BA}_{1,1}}{D(1,n)} \sum_{l=2}^{n} D(l,n)E(l) + \frac{1}{p^{BB}_{1,0} + p^{BA}_{1,1}}. \tag{2.37}$$

Hence, the average time to absorption starting from a single A individual randomly placed on the star, ${}^A T$, is given by

$$\begin{aligned} {}^A T &= \frac{1}{n+1} T_0^A + \frac{n}{n+1} T_1^B & (2.38) \\ &= \frac{1}{n+1} \left(\frac{\pi^{AA}_{0,1} + n\pi^{BA}_{1,1}}{D(1,n)} \sum_{l=2}^{n} D(l,n)E(l) + 1 + \frac{n}{p^{BB}_{1,0} + p^{BA}_{1,1}} \right). & (2.39) \end{aligned}$$

2.3.3 Mean time to fixation on the star graph

Let ${}^XF_i^A$ $\left({}^XF_i^B\right)$ denote the mean fixation time of individuals playing strategy X starting from the state with i As on the leaves and an A (a B) in the centre. Following the same method as in Antal and Scheuring (2006), ${}^AF_i^A$ and ${}^AF_i^B$ are given by the solution of the system

$${}^Az_i^A = p^{AA}_{i,i+1}\,{}^Az^A_{i+1} + p^{AB}_{i,i}\,{}^Az^B_i + \left(1 - p^{AA}_{i,i+1} - p^{AB}_{i,i}\right){}^Az^A_i + {}^AP^A_i, \quad 0 \le i \le n-1, \tag{2.40}$$

$${}^Az_i^B = p^{BA}_{i,i}\,{}^Az^A_i + p^{BB}_{i,i-1}\,{}^Az^B_{i-1} + \left(1 - p^{BA}_{i,i} - p^{BB}_{i,i-1}\right){}^Az^B_i + {}^AP^B_i, \quad 1 \le i \le n, \tag{2.41}$$

where ${}^Az_i^A = {}^AP_i^A\,{}^AF_i^A$ and ${}^Az_i^B = {}^AP_i^B\,{}^AF_i^B$. At the absorbing states,

$${}^Az_0^B = 0 \text{ because } {}^AP_0^B = 0, \tag{2.42}$$

$${}^Az_n^A = 0 \text{ because } {}^AF_n^A = 0. \tag{2.43}$$

Rearranging equations (2.40)–(2.41) we obtain the following system

$${}^Az_i^A = \pi^{AA}_{i,i+1}\,{}^Az^A_{i+1} + \pi^{AB}_{i,i}\,{}^Az^B_i + \frac{{}^AP^A_i}{p^{AA}_{i,i+1} + p^{AB}_{i,i}}, \quad 0 \le i \le n-1, \tag{2.44}$$

$${}^Az_i^B = \pi^{BA}_{i,i}\,{}^Az^A_i + \pi^{BB}_{i,i-1}\,{}^Az^B_{i-1} + \frac{{}^AP^B_i}{p^{BB}_{i,i-1} + p^{BA}_{i,i}}, \quad 1 \le i \le n. \tag{2.45}$$

Equation (2.44) can be written in the following form

$${}^Az_i^A = \frac{1}{\pi^{AA}_{i-1,i}}\,{}^Az^A_{i-1} - \frac{\pi^{AB}_{i-1,i-1}}{\pi^{AA}_{i-1,i}}\,{}^Az^B_{i-1} - \frac{{}^AP^A_{i-1}}{\pi^{AA}_{i-1,i}\left(p^{AA}_{i-1,i} + p^{AB}_{i-1,i-1}\right)}, \quad 1 \le i \le n-1. \tag{2.46}$$

Solving the system of equations (2.45)–(2.46) and (2.42)–(2.43) as before, we find

$${}^Az_i^A = D(1,i)\,{}^Az_1^A - \sum_{l=2}^{i} D(l,i)G(l), \quad 1 \le i \le n \tag{2.47}$$

$$\Rightarrow {}^AF_i^A = {}^AF_1^A - \frac{1}{{}^AP_i^A}\sum_{l=2}^{i} D(l,i)G(l), \qquad 1 \le i \le n, \tag{2.48}$$

where

$$G(l) = \frac{\pi^{AB}_{l-1,l-1}}{\pi^{AA}_{l-1,l}} \sum_{j=1}^{l-1}\left(\frac{{}^AP_j^B}{p^{BB}_{j,j-1} + p^{BA}_{j,j}} \prod_{k=j+1}^{l-1} \pi^{BB}_{k,k-1}\right) + \frac{{}^AP^A_{l-1}}{p^{AA}_{l-1,l}}. \tag{2.49}$$

For $i = n$, ${}^{A}F_n^A = 0$ and ${}^{A}P_n^A = 1$. Hence, from (2.48) we get

$$ {}^{A}F_1^A = \sum_{l=2}^{n} D(l,n)G(l). \tag{2.50}$$

Substituting (2.50) into (2.48) we find that ${}^{A}F_i^A$ $(1 \le i \le n)$ is given by

$$ {}^{A}F_i^A = \sum_{l=2}^{n} D(l,n)G(l) - \frac{1}{{}^{A}P_i^A} \sum_{l=2}^{i} D(l,i)G(l), \quad 1 \le i \le n. \tag{2.51}$$

From equations (2.45) and (2.42) we find

$$ {}^{A}z_i^B = \sum_{j=1}^{i} \pi_{j,j}^{BA} \left({}^{A}z_j^A + \frac{{}^{A}P_j^B}{p_{j,j}^{BA}} \right) \prod_{k=j+1}^{i} \pi_{k,k-1}^{BB}, \qquad 1 \le i \le n, \tag{2.52}$$

$$ \Rightarrow {}^{A}F_i^B = \frac{1}{{}^{A}P_i^B} \sum_{j=1}^{i} \pi_{j,j}^{BA} \left({}^{A}P_j^A \, {}^{A}F_j^A + \frac{{}^{A}P_j^B}{p_{j,j}^{BA}} \right) \prod_{k=j+1}^{i} \pi_{k,k-1}^{BB}, \quad 1 \le i \le n. \tag{2.53}$$

From (2.44) and (2.42) we have that for $i = 0$,

$$ {}^{A}z_0^A = \pi_{0,1}^{AA} \, {}^{A}z_1^A + {}^{A}P_0^A \Rightarrow {}^{A}F_0^A = \frac{\pi_{0,1}^{AA} \, {}^{A}P_1^A}{{}^{A}P_0^A} {}^{A}F_1^A + 1, \tag{2.54}$$

where we have used that $p_{0,1}^{AA} + p_{0,0}^{AB} = 1$. But ${}^{A}P_0^A = \pi_{0,1}^{AA} \, {}^{A}P_1^A$. Therefore, we obtain that

$$ {}^{A}F_0^A = {}^{A}F_1^A + 1 = \sum_{l=2}^{n} D(l,n)G(l) + 1. \tag{2.55}$$

From (2.53) we have that for $i = 1$,

$$ {}^{A}F_1^B = \frac{\pi_{1,1}^{BA} \, {}^{A}P_1^A}{{}^{A}P_1^B} {}^{A}F_1^A + \frac{1}{p_{1,0}^{BB} + p_{1,1}^{BA}}. \tag{2.56}$$

But ${}^{A}P_1^B = \pi_{1,1}^{BAA} P_1^A$. Therefore,

$$ {}^{A}F_1^B = {}^{A}F_1^A + \frac{1}{p_{1,0}^{BB} + p_{1,1}^{BA}} = \sum_{l=2}^{n} D(l,n)G(l) + \frac{1}{p_{1,0}^{BB} + p_{1,1}^{BA}}. \tag{2.57}$$

The average fixation time of a single A individual randomly placed on the star, ${}^{A}F$, is given by

$$ {}^{A}F = \frac{1}{n+1} {}^{A}F_0^A + \frac{n}{n+1} {}^{A}F_1^B = \frac{1}{n+1} \left((n+1) \sum_{l=2}^{n} D(l,n)G(l) + 1 + \frac{n}{p_{1,0}^{BB} + p_{1,1}^{BA}} \right). \tag{2.58}$$

Note that by symmetry, replacing $p^{AA}_{i,i+1}$ by $p^{BB}_{n-i,n-i-1}$, $p^{AB}_{i,i}$ by $p^{BA}_{n-i,n-i}$, $p^{BB}_{i,i-1}$ by $p^{AA}_{n-i,n-i+1}$, $p^{BA}_{i,i}$ by $p^{AB}_{n-i,n-i}$, ${}^{A}P^{A}_{i}$ by $1-{}^{A}P^{B}_{n-i}={}^{B}P^{B}_{n-i}$ and ${}^{A}P^{B}_{i}$ by $1-{}^{A}P^{A}_{n-i}={}^{B}P^{A}_{n-i}$ in the above formulae, we find the respective formulae of the fixation probability and absorption and fixation times of B individuals when they are introduced into a population of As.

2.4 Evolutionary games on the complete graph, the circle and the star graph under the update rules of the invasion process

In this section, we investigate the evolutionary process on the complete graph, the circle and the star graph following the update rules of the commonly used IP (see Section 1.5). Here, the fitness of each individual is assumed to be equal to $f = f_b + wP$, a linear function of the average payoff P obtained by the games played with neighbouring individuals. f_b is a constant background fitness and $w \in [0,\infty)$ represents the intensity of selection which determines the contribution of P to fitness. When $w \to 0$, the payoff P of each individual has a small contribution to the overall fitness and we have so-called *weak selection*. Thus, in this case the fitness differences between the different types of individuals are small and the stochastic effects of the process are more pronounced. When $w = 0$ all individuals have the same fitness and thus we have the case of neutral drift. Finally, when $w \to \infty$ the contribution of P to the fitness becomes arbitrarily large, and the effect of background fitness f_b becomes negligible. Although the intensity of selection is irrelevant in the traditional evolutionary game dynamics (since this cancels out), it is very important in stochastic evolutionary dynamics in finite populations.

Note that since in the evolutionary process the probability of an individual being chosen for reproduction is proportional to its fitness and this probability must be non-negative, the fitness of individuals must be non-negative.

Depending on the nature of the game and the evolutionary process, the individual's payoff, P, can be considered in different ways. Alternatively, for example, the total payoff of an individual could be considered as just the sum of the payoffs obtained by each game played with each of its neighbours (accumulated payoff). Although the choice of computing the payoff between these two ways does not influence the outcome of the evolutionary process on regular graphs where each individual has the same degree (for example circles and complete graphs), it is crucial on irregular graphs and depending on the evolutionary dynamics and the population structure, might yield remarkably different outcomes (see for example, Santos and Pacheco, 2006; Masuda, 2007; Tomassini *et al.*, 2007; Szolnoki *et al.*, 2008). For example, in the IP on a star graph the fitness of the individual in the central vertex is significantly diminished when taking the average payoff, and the chance of this individual to survive and reproduce is reduced. In contrast, the contribution of the accumulated payoff to the fitness makes the individual in the centre much fitter (given positive payoffs) and its chance of survival and reproduction is higher. However, in evolutionary dynamics where in each time step an individual first reproduces or dies at random, the fitness of the central individual does not matter and since the individuals on the leaves interact just with the individual in the centre, the way of computing the payoff is irrelevant. In this work, assuming that at each time step individuals interact with neighbouring individuals at the same rate, the total payoff of each individual in each step is considered to be the average of the obtained accumulated payoff. Alternative fitness functions have also been considered, for example the exponential function of the payoff, $f = \exp(wP)$ (Traulsen *et al.*, 2008). These fitness functions are usually used for modelling the evolution of finite structured populations represented by graphs. Different fitness functions have also been introduced for the modelling of evolutionary dynamics beyond the framework of pairwise interactions between individuals (e.g., Broom and Rychtář, 2012).

For each of the graphs we consider, the complete graph, the circle and the star graph, we first derive the transition probabilities following the update rules of the IP and then, using the formulae of Sections 2.2 and 2.3, we derive the exact solutions of the fixation probability, the mean absorption and fixation time as well as the mean number of transitions to absorption and fixation in this process.

Let us denote the following terms, which are useful in subsequent calculations. Let

$$\mu_i = \frac{i\alpha + (N-1-i)\beta}{N-1}, \tag{2.59}$$

$$\nu_i = \frac{i\gamma + (N-1-i)\delta}{N-1} \tag{2.60}$$

be the fitness of an A and a B individual, respectively, that is neighbouring with i As and $N-1-i$ Bs (this is equal to the fitness of an individual in the center of a star with i As on the leaves, or an individual with i neighbouring As anywhere in a complete graph). We have set $\alpha = f_b + wa$, $\beta = f_b + wb$, $\gamma = f_b + wc$ and $\delta = f_b + wd$.

2.4.1 Evolutionary games on the complete graph under the update rules of the invasion process

On a complete graph consisting of i individuals playing strategy A and $N-i$ individuals playing B, the fitness of an A individual is $f_A = f_b + wP_A$ and that of a B individual $f_B = f_b + wP_B$, where

$$P_A = \frac{(i-1)a + (N-i)b}{N-1}, \tag{2.61}$$

$$P_B = \frac{ic + (N-i-1)d}{N-1}. \tag{2.62}$$

Note that these payoffs are identical to the payoffs obtained by an A and a B individual, respectively, in a homogeneous well-mixed population of size N since an A individual interacts another A with probability $(i-1)/(N-1)$ and a B with probability $(N-i)/(N-1)$, while a B individual interacts an A with probability $i/(N-1)$ and a B with probability $(N-i-1)/(N-1)$.

Transition probabilities

The number of $i \in [1, N-1]$ A individuals on a complete graph in processes without mutation can increase by one if the offspring of any A replaces any B individual. Similarly, their number decreases by one if the offspring of any of the $N-i$ B individuals replaces any of the A individuals. Following the rules of the IP, the probabilities of the number of i A individuals increasing or decreasing on a complete graph are given by

$$\begin{aligned} p_{i,i+1} &= \frac{i f_A}{i f_A + (N-i) f_B} \cdot \frac{N-i}{N-1} \\ &= \frac{i(N-i)\mu_{i-1}}{(N-1)\big(i\mu_{i-1} + (N-i)\nu_i\big)}, \quad 1 \le i \le N-1, \end{aligned} \tag{2.63}$$

$$\begin{aligned} p_{i,i-1} &= \frac{(N-i) f_B}{i f_A + (N-i) f_B} \cdot \frac{i}{N-1} \\ &= \frac{i(N-i)\nu_i}{(N-1)\big(i\mu_{i-1} + (N-i)\nu_i\big)}, \quad 1 \le i \le N-1, \end{aligned} \tag{2.64}$$

and zero in every other case. The probability of the system remaining at the same state is obviously $p_{i,i} = 1 - p_{i,i+1} - p_{i,i-1} \ \forall \ i \in [0, N]$.

Fixation probability

Substituting the transition probabilities (2.63)–(2.64) into (1.27) we get that the fixation probability of $i \in [1, N]$ A individuals introduced on a complete graph where vertices are occupied by B individuals is given by

$$ {}^{A}P_i = \frac{A(0, i-1)}{A(0, N-1)}, \tag{2.65} $$

where

$$ A(j, m) = \sum_{l=j}^{m} \prod_{k=j+1}^{l} \frac{\nu_k}{\mu_{k-1}}. \tag{2.66} $$

Mean time to absorption

The mean time before absorption occurs starting from $i \in [1, N]$ individuals playing strategy A on a complete graph is given by the formula (1.34). Substituting the transition probabilities (2.63)–(2.64) into this we obtain

$$ T_i = {}^{A}P_i \sum_{j=1}^{N-1} h(j) A(j, N-1) - \sum_{j=1}^{i-1} h(j) A(j, i-1), \tag{2.67} $$

where

$$ h(j) = \frac{(N-1)\big(j\mu_{j-1} + (N-j)\nu_j\big)}{j(N-j)\mu_{j-1}}. \tag{2.68} $$

Mean time to fixation

The substitution of the transition probabilities (2.63)–(2.64) into (1.35) give us the mean fixation time of $i \in [1, N]$ A individuals when the update rules of the IP are applied. This is given by the formula

$$ {}^{A}F_i = \sum_{j=1}^{N-1} {}^{A}P_j h(j) A(j, N-1) - \frac{1}{{}^{A}P_i} \sum_{j=1}^{i-1} {}^{A}P_j h(j) A(j, i-1). \tag{2.69} $$

Mean number of transitions before absorption/fixation occurs

Here, we count just the number of time steps in which the number of A individuals either increases or decreases by one. Hence, we condition on the number of As in every step not being the same with that in the previous step, i.e. $p_{i,i+1} + p_{i,i-1} = 1$. The non-zero conditional probabilities of transition on the complete graph following the rules of the IP are given by

$$\pi_{i,i+1} = \frac{\mu_{i-1}}{\mu_{i-1}+\nu_i}, \quad 1 \le i \le N-1, \tag{2.70}$$

$$\pi_{i,i-1} = \frac{\nu_i}{\mu_{i-1}+\nu_i}, \quad 1 \le i \le N-1. \tag{2.71}$$

Substituting the transition probabilities (2.70)–(2.71) into the formula (1.34), where $p_{i,j} = \pi_{i,j}\ \forall\ i,j$, we find the mean number of transitions needed before absorption occurs starting from $i \in [1,N]$ individuals playing strategy A on a complete graph.

Similarly, the mean number of transitions before the fixation of $i \in [1,N]$ individuals playing strategy A is obtained by substituting (2.70)–(2.71) into (1.35).

2.4.2 Evolutionary games on the circle graph under the update rules of the invasion process

Transition probabilities

On the circle, every individual is connected either to two individuals playing strategy A, to two individuals playing strategy B, or to one individual playing each of the strategies. An individual between two As has fitness α if it is an A individual and fitness γ if it is a B individual. Note that a B individual is between two As whenever it is the only individual playing B in the population. An individual between two Bs has fitness β if it is an A individual and fitness δ if it is a B individual. As before, an A individual is between two Bs only if it is the only one of its type in the population. Finally, an individual between an A and a B has fitness equal to $(\alpha+\beta)/2$ when playing strategy A and fitness equal to $(\gamma+\delta)/2$ when playing strategy B. The number of A individuals can increase (decrease) by one only if an A (a B) individual on the boundary between the two segments, one consisting of As and the other of Bs, reproduces and its offspring replaces a connected individual playing the other strategy. The non-zero probabilities of moving from one state to another on the circle under the rules of the IP are the following

$$p_{1,2} = \frac{\beta}{\beta+(N-1)\nu_1}, \tag{2.72}$$

$$p_{i,i+1} = \frac{\alpha+\beta}{2\big((i-1)\alpha+\beta+\gamma+(N-1-i)\delta\big)}, \quad 2 \le i \le N-1, \tag{2.73}$$

$$p_{i,i-1} = \frac{\gamma+\delta}{2\big((i-1)\alpha+\beta+\gamma+(N-1-i)\delta\big)}, \quad 1 \le i \le N-2, \tag{2.74}$$

$$p_{N-1,N-2} = \frac{\gamma}{(N-1)\mu_{N-2}+\gamma}, \tag{2.75}$$

and zero in any other case. The probability to remain in the same state is $p_{i,i} = 1 - p_{i,i+1} - p_{i,i-1}$, $\forall\ i \in [0,N]$.

Fixation probability

Substituting the transition probabilities (2.72)–(2.75) into (1.27) we obtain that, in the IP, the fixation probability of $i \in [1,N-1]$ A individuals on the circle, ${}^{A}P_i$, is given by

$${}^{A}P_i = \frac{1+\frac{\gamma+\delta}{2\beta}\sum\limits_{j=0}^{i-2}\left(\frac{\gamma+\delta}{\alpha+\beta}\right)^{j}}{1+\frac{\gamma+\delta}{2\beta}B(1)}, \quad N \ge 3, \tag{2.76}$$

where

$$B(j) = \sum_{k=0}^{N-2-j}\left(\frac{\gamma+\delta}{\alpha+\beta}\right)^{k} + \left(\frac{\gamma+\delta}{\alpha+\beta}\right)^{N-2-j}\frac{2\gamma}{\alpha+\beta}. \tag{2.77}$$

Mean time to absorption

The mean time to absorption on a circle is given by formula (1.34). Substituting the transition probabilities (2.72)–(2.75) we obtain that in the IP the mean time to absorption starting from $i \in [1,N-1]$ A individuals, T_i, is given by

$$T_i = {}^{A}P_i C_1(N) - C_1(i), \tag{2.78}$$

where

$$C_1(N) = \frac{B(1)}{p_{1,2}} + \sum_{j=2}^{N-2}\frac{B(j)}{p_{j,j+1}} + \frac{1}{p_{N-1,N}}, \tag{2.79}$$

$$C_1(i) = \frac{1}{p_{1,2}}\sum_{k=0}^{i-2}\left(\frac{\gamma+\delta}{\alpha+\beta}\right)^{k} + \sum_{j=2}^{i-1}\frac{1}{p_{j,j+1}}\sum_{k=0}^{i-j-1}\left(\frac{\gamma+\delta}{\alpha+\beta}\right)^{k}. \tag{2.80}$$

Mean time to fixation

The mean number of time steps before the fixation of A individuals starting from $i \in [1,N]$ As on the circle is given by formula (1.35). In the IP it is found that

$${}^{A}F_i = \frac{B(1)}{p_{1,2}}{}^{A}P + \sum_{j=2}^{N-2}\frac{B(j)}{p_{j,j+1}}{}^{A}P_j + \frac{{}^{A}P_{N-1}}{p_{N-1,N}} - \frac{1}{{}^{A}P_i}C_2(i) \tag{2.81}$$

where

$$C_2(i) = \frac{{}^{A}P}{p_{1,2}} \sum_{k=0}^{i-2} \left(\frac{\gamma+\delta}{\alpha+\beta}\right)^k + \sum_{j=2}^{i-1} \frac{{}^{A}P_j}{p_{j,j+1}} \sum_{k=0}^{i-j-1} \left(\frac{\gamma+\delta}{\alpha+\beta}\right)^k. \tag{2.82}$$

Mean number of transitions before absorption/fixation occurs

In the case where the offspring of each individual can replace an individual of the other type only, the process on the circle can be thought of as a process where only the individuals on the boundaries of two segments of the different types can compete for reproduction. These are the one A individual and the two Bs when there is only one A individual in the population, the two As and the two Bs on the boundaries when there are at least two As and two Bs, and the two As and the one B, when there is only one B individual in the population. Hence, in this case, the conditional probabilities of transition on the circle are given by

$$\pi_{1,2} = \frac{2\beta}{2\beta+\gamma+\delta}, \tag{2.83}$$

$$\pi_{1,0} = \frac{\gamma+\delta}{2\beta+\gamma+\delta}, \tag{2.84}$$

$$\pi_{i,i+1} = \frac{\alpha+\beta}{\alpha+\beta+\gamma+\delta}, \quad 2 \le i \le N-2, \tag{2.85}$$

$$\pi_{i,i-1} = \frac{\gamma+\delta}{\alpha+\beta+\gamma+\delta}, \quad 2 \le i \le N-2, \tag{2.86}$$

$$\pi_{N-1,N} = \frac{\alpha+\beta}{\alpha+\beta+2\gamma}, \tag{2.87}$$

$$\pi_{N-1,N-2} = \frac{2\gamma}{\alpha+\beta+2\gamma}, \tag{2.88}$$

and zero in any other case.

Substituting the transition probabilities (2.83)–(2.88) into the formula (1.34), where $p_{i,j} = \pi_{i,j}\ \forall\ i,j$, one can obtain the mean number of transitions before absorption occurs when starting from $i \in [1, N-1]$ A individuals on a circle. The mean number of transitions before $i \in [1, N]$ A individuals fixate on the circle is obtained by substituting (2.83)–(2.88) into the formula (1.35).

2.4.3 Evolutionary games on the star graph under the update rules of the invasion process

On a star graph with i As and $n-i$ Bs on the leaves, the fitnesses of an A and a B individual placed in the centre, $f_{Ac}(i)$ and $f_{Bc}(i)$ respectively, are given by

$$f_{Ac}(i) = \frac{i\alpha + (n-i)\beta}{n}, \tag{2.89}$$

$$f_{Bc}(i) = \frac{i\gamma + (n-i)\delta}{n}. \tag{2.90}$$

The fitness of an A (a B) individual on the leaves is equal to α (γ) when playing against an A individual in the centre and β (δ) when playing against a B individual in this position.

Transition probabilities

The number of A (B) individuals on the leaves of a star can increase by one, and thus the number of Bs (As) decrease by one, if a B (an A) individual on the leaves (given there is one) is replaced by the offspring of an A (a B) individual in the centre. An individual in the centre changes type whenever an individual of the other type is chosen for reproduction.

The transition probabilities between the different states on the star graph in the IP are given by

$$p_{i,i+1}^{AA} = \frac{f_{Ac}(i)}{f_{Ac}(i) + i\alpha + (n-i)\gamma} \cdot \frac{n-i}{n} = \frac{\mu_i}{i\alpha + (n-i)\gamma + \mu_i} \cdot \frac{n-i}{n}, \quad 0 \le i \le n-1, \tag{2.91}$$

$$p_{i,i}^{AB} = \frac{(n-i)\gamma}{f_{Ac}(i) + i\alpha + (n-i)\gamma} = \frac{(n-i)\gamma}{i\alpha + (n-i)\gamma + \mu_i}, \quad 0 \le i \le n-1, \tag{2.92}$$

$$p_{i,i-1}^{BB} = \frac{f_{Bc}(i)}{f_{Bc}(i) + i\beta + (n-i)\delta} \cdot \frac{i}{n} = \frac{\nu_i}{i\beta + (n-i)\delta + \nu_i} \cdot \frac{i}{n}, \quad 1 \le i \le n, \tag{2.93}$$

$$p_{i,i}^{BA} = \frac{i\beta}{f_{Bc}(i) + i\beta + (n-i)\delta} = \frac{i\beta}{i\beta + (n-i)\delta + \nu_i}, \quad 1 \le i \le n, \tag{2.94}$$

and zero in any other case. $p_{i,i}^{AA} = 1 - p_{i,i+1}^{AA} - p_{i,i}^{AB}\ \forall\, i \in [0,n]$ and $p_{i,i}^{BB} = 1 - p_{i,i-1}^{BB} - p_{i,i}^{BA}\ \forall\, i \in [0,n]$.

Fixation probability

Substituting the transition probabilities (2.91)–(2.94) into the formulae (2.19) and (2.20) we find the fixation probability of i $(1 \le i \le n)$ A individuals on the leaves and an A individual in the centre, ${}^{A}P_i^A$, and the fixation probability of i $(1 \leq i \leq n)$ A individuals on the leaves with a B individual in the centre, ${}^{A}P_i^B$, respectively. These are given by the following formulae.

$$ {}^{A}P_i^A = \frac{D(1,i)}{D(1,n)}, \qquad 1 \leq i \leq n, \tag{2.95} $$

$$ {}^{A}P_i^B = \sum_{j=1}^{i} \frac{n\beta}{n\beta + \nu_j} {}^{A}P_j^A \prod_{k=j+1}^{i} \frac{\nu_k}{n\beta + \nu_k}, \quad 1 \leq i \leq n, \tag{2.96} $$

where

$$ D(l,m) = 1 + \sum_{j=l}^{m-1} \frac{n\gamma}{n\gamma + \mu_j} \prod_{k=l}^{j} \frac{\nu_k\,(n\gamma + \mu_k)}{\mu_k\,(n\beta + \nu_k)}. \tag{2.97} $$

From equation (2.21), we obtain that ${}^{A}P_0^A$ is given by

$$ {}^{A}P_0^A = \frac{\beta}{(\beta + n\gamma)} \frac{1}{D(1,n)}. \tag{2.98} $$

Using the formula (2.23), we get the average fixation probability of a single A individual randomly placed on the star, ${}^{A}P$, when the update rules of the IP are followed being given by

$$ {}^{A}P = \frac{1}{n+1} \left(\frac{n^2\beta}{n\beta + \nu_1} + \frac{\beta}{\beta + n\gamma} \right) \frac{1}{D(1,n)}. \tag{2.99} $$

Mean time to absorption

The mean time to absorption starting from i $(1 \leq i \leq n)$ A individuals on the leaves and an A individual in the centre, T_i^A, and the mean time to absorption starting from i A individuals on the leaves with a B individual in the centre, T_i^B, in the IP are given by the following formulae.

$$ T_i^A = {}^{A}P_i^A \sum_{l=2}^{n} D(l,n)E(l) - \sum_{l=2}^{i} D(l,i)E(l), \qquad 1 \leq i \leq n, \tag{2.100} $$

$$ T_i^B = \sum_{j=1}^{i} \left(\frac{n\beta}{n\beta + \nu_j} T_j^A + \lambda_j \right) \prod_{k=j+1}^{i} \frac{\nu_k}{n\beta + \nu_k}, \quad 1 \leq i \leq n, \tag{2.101} $$

where

$$ E(l) = \frac{n\gamma}{\mu_{l-1}} \sum_{j=1}^{l-1} \left(\lambda_j \prod_{k=j+1}^{l-1} \frac{\nu_k}{n\beta + \nu_k} \right) + \kappa_{l-1} \tag{2.102} $$

and

$$\kappa_i = \frac{n}{n-i} \cdot \frac{i\alpha + (n-i)\gamma + \mu_i}{\mu_i}, \tag{2.103}$$

$$\lambda_i = \frac{n}{i} \cdot \frac{i\beta + (n-i)\delta + \nu_i}{n\beta + \nu_i}. \tag{2.104}$$

These have been derived by substituting the transition probabilities (2.91)–(2.94) into the formulae (2.34) and (2.35), respectively. From (2.36) we derive that the mean time to absorption starting from a single individual placed in the centre of the star is given by

$$T_0^A = \frac{\beta}{\beta + n\gamma} \frac{1}{D(1,n)} \sum_{l=2}^{n} D(l,n)E(l) + 1. \tag{2.105}$$

Using (2.39), we obtain that the average time to absorption starting from a single A individual randomly placed on the star, ${}^{A}T$, is given by

$${}^{A}T = \frac{1}{n+1}\left(\left(\frac{n^2\beta}{n\beta + \nu_1} + \frac{\beta}{\beta + n\gamma}\right)\frac{1}{D(1,n)}\sum_{l=2}^{n} D(l,n)E(l) + n\lambda_1 + 1\right). \tag{2.106}$$

Mean time to fixation

Substituting the transition probabilities (2.91)–(2.94) into the formulae (2.51) and (2.53), we obtain that the fixation time of i $(1 \le i \le n)$ A individuals on the leaves and an A individual in the centre, ${}^{A}F_i^A$, and the fixation time of i $(1 \le i \le n)$ A individuals on the leaves with a B in the centre, ${}^{A}F_i^B$, are given respectively by

$${}^{A}F_i^A = \sum_{l=2}^{n} D(l,n)G(l) - \frac{1}{{}^{A}P_i^A}\sum_{l=2}^{i} D(l,i)G(l), \qquad 1 \le i \le n, \tag{2.107}$$

$${}^{A}F_i^B = \frac{1}{{}^{A}P_i^B}\sum_{j=1}^{i}\left(\frac{n\beta}{n\beta + \nu_j}{}^{A}P_j^A\,{}^{A}F_j^A + \lambda_j{}^{A}P_j^B\right)\prod_{k=j+1}^{i}\frac{\nu_k}{n\beta + \nu_k}, \quad 1 \le i \le n, \tag{2.108}$$

where

$$G(l) = \frac{n\gamma}{\mu_{l-1}}\sum_{j=1}^{l-1}\left(\lambda_j{}^{A}P_j^B\prod_{k=j+1}^{l-1}\frac{\nu_k}{n\beta + \nu_k}\right) + \kappa_{l-1}{}^{A}P_{l-1}^A.$$

From (2.55), the mean fixation time of a single A individual placed in the centre of the star graph, ${}^{A}F_0^A$, is given by

$${}^{A}F_0^A = \sum_{l=2}^{n} D(l,n)G(l) + 1. \tag{2.109}$$

The average fixation time of a single A individual randomly placed on the star, ${}^{A}F$, when the update rules of the IP are followed, is given by

$$ {}^{A}F = \frac{1}{n+1}\left((n+1)\sum_{l=2}^{n} D(l,n)G(l) + n\lambda_1 + 1\right). \tag{2.110} $$

Mean number of transitions before absorption/fixation occurs

On the star graph, if the offspring of an individual can replace only an individual of the other type, then $p^{AA}_{i,i+1} + p^{AB}_{i,i} = 1, \forall\, i \in [0, n-1]$, and $p^{BB}_{i,i-1} + p^{BA}_{i,i} = 1, \forall\, i \in [1, n]$. Hence, in this case the transition probabilities are given by

$$ \pi^{AA}_{i,i+1} = \frac{i\alpha + (n-i)\beta}{i\alpha + (n-i)\beta + n^2\gamma}, \quad 0 \le i \le n-1, \tag{2.111} $$

$$ \pi^{AB}_{i,i} = \frac{n^2\gamma}{i\alpha + (n-i)\beta + n^2\gamma}, \quad 0 \le i \le n-1, \tag{2.112} $$

$$ \pi^{BB}_{i,i-1} = \frac{i\gamma + (n-i)\delta}{n^2\beta + i\gamma + (n-i)\delta}, \quad 1 \le i \le n, \tag{2.113} $$

$$ \pi^{BA}_{i,i} = \frac{n^2\beta}{n^2\beta + i\gamma + (n-i)\delta}, \quad 1 \le i \le n, \tag{2.114} $$

and zero in any other case. Substituting the transition probabilities (2.111)–(2.114) into the formulae (2.34), (2.35) and (2.36), where $p^{XY}_{i,j} = \pi^{XY}_{i,j}\ \forall\ i,j$ and $\forall\ X,Y \in [A,B]$, one can derive the mean number of transitions before absorption occurs starting from every possible state on the star graph. The mean number of transitions before A individuals fixate on the star can be similarly obtained by substituting (2.111)–(2.114) into the formulae (2.51), (2.53) and (2.55).

2.5 Favoured strategies on the complete graph, the circle and the star graph under the update rules of the invasion process

In evolutionary games, the comparison of the fixation probability of a single individual playing strategy A in a population of individuals playing strategy B, ${}^{A}P$, with that of an individual playing strategy B in a population of individuals playing A, ${}^{B}P$, is of interest. Strategy A is said to be favoured by natural selection over strategy B if it is more abundant (its average frequency is higher) in the stationary distribution of the stochastic process. In evolutionary processes where there is no mutation, the stationary distribution is non-zero only on the absorbing states, where the population consists only of individuals playing one of the two strategies. Hence, in this case, the condition for strategy A to be favoured over strategy B reduces to the condition ${}^{A}P > {}^{B}P$. When ${}^{A}P = {}^{B}P$, an A individual introduced into a population of Bs does equally well as a B individual when it is introduced into a population of As. The conditions under which one strategy is favoured over the other have been found for several graphs and update rules under the assumption of weak selection (see Tarnita *et al.*, 2009). In general, many analytic results have been derived in the limit of weak selection, because in this limit complicated non-linear functions can be approached by linear functions, making the analytic investigation easier. In this section, we derive the appropriate (general) conditions for strategy A to be favoured over strategy B on the complete graph, the circle and the star graph.

On a complete graph and a circle, the fixation probability of a single B individual, ${}^{B}P$, is equal to the probability that $N-1$ A individuals do not fixate but die out. Hence,

$$\begin{aligned} {}^{B}P &= 1 - {}^{A}P_{N-1} && (2.115)\\ &= 1 - \frac{1 + \sum_{j=1}^{N-2} \prod_{k=1}^{j} q_k}{1 + \sum_{j=1}^{N-1} \prod_{k=1}^{j} q_k} = \frac{\prod_{k=1}^{N-1} q_k}{1 + \sum_{j=1}^{N-1} \prod_{k=1}^{j} q_k} = {}^{A}P \prod_{k=1}^{N-1} q_k && (2.116)\\ \Rightarrow \frac{{}^{A}P}{{}^{B}P} &= \prod_{k=1}^{N-1} \frac{p_{k,k+1}}{p_{k,k-1}}. && (2.117) \end{aligned}$$

Let $\rho_{\mathrm{UR}}^{\mathrm{G}}$ denote the ratio ${}^{A}P/{}^{B}P$ under the update rule UR on the graph G. Hence, a strategy A is favoured over a strategy B on the graph G under the update rule UR if $\rho_{\mathrm{UR}}^{\mathrm{G}} > 1$.

On a complete graph, substituting the transition probabilities in the IP, (2.63)–(2.64), into (2.117) we obtain that

$$\rho_{\mathrm{IP}}^{\mathrm{CG}} = \prod_{k=1}^{j} \frac{(k-1)\alpha + (N-k)\beta}{k\gamma + (N-k-1)\delta} = \exp\left(\sum_{k=1}^{N-1} \ln \frac{(k-1)\alpha + (N-k)\beta}{k\gamma + (N-k-1)\delta} \right). \quad (2.118)$$

For large N, the sum in (2.118) can be approached by the following integral

$$I = \int_1^N \ln\left(\frac{(\alpha-\beta)k + N\beta}{(\gamma-\delta)k + N\delta} \right) dk \approx N \int_0^1 \ln\left(\frac{\beta}{\delta} \frac{(\alpha/\beta - 1)x + 1}{(\gamma/\delta - 1)x + 1} \right) dx. \quad (2.119)$$

Evaluating the integral we find that for large N, I is approximated by

$$I = \ln\left(\frac{\alpha}{\delta}\frac{\left(\frac{\alpha}{\beta}\right)^{\left(\frac{\beta}{\alpha-\beta}\right)}}{\left(\frac{\delta}{\gamma}\right)^{\left(\frac{\gamma}{\delta-\gamma}\right)}}\right), \quad \alpha \neq \beta,\ \gamma \neq \delta. \tag{2.120}$$

Thus, on a large complete graph we find that under the IP

$$\ln(\rho_{\text{IP}}^{\text{CG}}) \approx \ln\left(\frac{\alpha}{\delta}\frac{\left(\frac{\alpha}{\beta}\right)^{\left(\frac{\beta}{\alpha-\beta}\right)}}{\left(\frac{\delta}{\gamma}\right)^{\left(\frac{\gamma}{\delta-\gamma}\right)}}\right)^{N}, \quad \alpha \neq \beta,\ \gamma \neq \delta \tag{2.121}$$

(see Fudenberg *et al.*, 2006; Antal and Scheuring, 2006). Hence, As are favoured over Bs if $\alpha\left(\frac{\alpha}{\beta}\right)^{\left(\frac{\beta}{\alpha-\beta}\right)} > \delta\left(\frac{\delta}{\gamma}\right)^{\left(\frac{\gamma}{\delta-\gamma}\right)}$. In the limit of weak selection, $w \to 0$, it follows that individuals playing strategy A are favoured over individuals playing B if $a+b > c+d$. This is the condition for strategy A to be the risk dominant strategy. Note that $a+b > c+d$ does not imply that $\alpha\left(\frac{\alpha}{\beta}\right)^{\left(\frac{\beta}{\alpha-\beta}\right)} > \delta\left(\frac{\delta}{\gamma}\right)^{\left(\frac{\gamma}{\delta-\gamma}\right)}$.

On a circle, substituting the transition probabilities in the IP, (2.72)–(2.75), into (2.117) we obtain that

$$\rho_{\text{IP}}^{\text{C}} = \frac{\beta}{\gamma}\left(\frac{\alpha+\beta}{\gamma+\delta}\right)^{N-2}. \tag{2.122}$$

Hence, on a large circle, A individuals are favoured over B individuals if the simple condition $a+b > c+d$ holds.

On a star graph graph with n leaves, a single B individual placed on a leaf has fixation probability equal to the probability an A in the centre and $n-1$ As on the leaves are eliminated. Similarly, a single B placed in the centre has fixation probability equal to the extinction probability of n As on the leaves. Hence,

$$^{B}P = \frac{1}{n+1}\left(1 - {}^{A}P_{n}^{B}\right) + \frac{n}{n+1}\left(1 - {}^{A}P_{n-1}^{A}\right). \tag{2.123}$$

Using (2.5)–(2.6), the fact that $\pi_{i,i+1}^{AA} + \pi_{i,i}^{AB} = 1 = \pi_{i,i}^{BA} + \pi_{i,i-1}^{BB}$ and also (2.19) for $i = n-1$, (2.123) can be written as

$$^{B}P = \frac{1}{n+1}\left(\pi_{n,n-1}^{BB} + n\pi_{n-1,n-1}^{AB}\right)\left(\prod_{k=1}^{n-1}\frac{\pi_{k,k-1}^{BB}}{\pi_{k,k+1}^{AA}}\right)\frac{1}{D(1,n)}. \tag{2.124}$$

Using (2.124) and (2.23) we obtain

$$\rho_{\text{UR}}^{\text{S}} = \frac{\pi_{0,1}^{AA} + n\pi_{1,1}^{BA}}{\pi_{n,n-1}^{BB} + n\pi_{n-1,n-1}^{AB}} \prod_{k=1}^{n-1} \frac{\pi_{k,k+1}^{AA}}{\pi_{k,k-1}^{BB}}. \tag{2.125}$$

In the IP, as shown in Appendix B.2.1, for large n we find

$$\rho_{\text{IP}}^{\text{S}} > 1 \Leftrightarrow \alpha\beta\left(\frac{\alpha}{\beta}\right)^{\frac{\beta}{\alpha-\beta}} > \gamma\delta\left(\frac{\delta}{\gamma}\right)^{\frac{\gamma}{\delta-\gamma}}, \quad \alpha \neq \beta,\ \gamma \neq \delta. \tag{2.126}$$

In the case of weak selection, from the condition (2.126), it is obtained that on a large star strategy A is favoured over strategy B if and only if $a+b > c+d$. This agrees with the result of Tarnita *et al.* (2009). Note that $a+b$ might be less than $c+d$ but $\alpha\beta\left(\frac{\alpha}{\beta}\right)^{\frac{\beta}{\alpha-\beta}}$ higher than $\gamma\delta\left(\frac{\delta}{\gamma}\right)^{\frac{\gamma}{\delta-\gamma}}$.

In general, it has been shown (Tarnita *et al.*, 2009) that in a game between two strategies, A and B, played on a structured population, in the limit of weak selection strategy A is favoured over strategy B (given that three natural assumptions are satisfied) if the linear inequality

$$\sigma a + b > c + \sigma d \tag{2.127}$$

holds. σ is a parameter that depends on the population structure, the population size, the update rule and the mutation rate, but not on the payoff values.

2.6 Numerical examples

2.6.1 The constant fitness case

Although our emphasis will be on the frequency dependent fitness case which is considered in the next section, we start by the case where the individuals of the population have constant fitness. Assume that mutant A individuals have relative constant fitness equal to r and resident B individuals have fitness equal to 1. In this case, the fitness of each individual depends only on its type (mutant or resident) and is not affected by its interactions with other members of the population. Therefore, the configuration of the population is irrelevant. This case can be considered as a special case of an evolutionary game with $a = b = r$, $c = d = 1$, $w = 1$ and $f_b = 0$. We consider and compare the fixation probability, the absorption and fixation times as well as the mean number of transitions before absorption and fixation occur when a single mutant is introduced on the three different structures. Many of the observations will then be carried over to the more complicated case of frequency dependent fitness.

The fixation probability of a single mutant

Here, we compare the fixation probability of a single mutant on a complete graph and a circle, which in this case is identical to the fixation probability in the Moran process and on every circulation graph (see Lieberman *et al.*, 2005), with the average fixation probability of a mutant on a star. This comparison has also been considered in Broom and Rychtář (2008).

The fixation probability of an advantageous mutant ($r > 1$) on the star is generally greater than the fixation probability in the Moran process. Similarly the fixation probability of a disadvantageous mutant ($r < 1$) on the star is lower than the fixation probability in the Moran process. Hence, the star graph enhances selection in the evolutionary process when the rules of the IP are followed. On the star, the average fixation probability of an advantageous mutant increases with the increase of the population size and approaches the solution (1.38) derived by Lieberman *et al.* (2005) in the case of very large populations. This tends to a constant given by $1 - 1/r^2$. In contrast, the fixation probability in the Moran process decreases and converges to $1 - 1/r$ (see Figure 2.2a). In the case where a disadvantageous mutant invades, the increase of the number of individuals reduces the chance of mutants to fixate to zero, both on the star and in the Moran process.

Note that on a star graph, the variation of the fixation probability of a mutant on the leaves is very different from that of the fixation probability of a mutant in the centre as the population size increases. In particular, in the IP, if the first mutant is placed in the centre, the larger the population size, the larger the probability of a resident individual on the leaves being chosen for reproduction, and thus the higher the probability for the mutant in the centre being killed and replaced by the offspring of the resident individual. Hence, the fixation probability of a mutant in the centre decreases with the increase of the population size. However, if the first mutant is placed on the leaves, it has a higher chance of being chosen for reproduction than the resident in the centre, and this chance increases as the population size increases resulting in an increase of the probability of mutant fixation. Since the probability the first mutant to be placed on the leaves is higher and increases with the population size, the average fixation probability increases as the population size increases (at least for not very small populations).

For constant population size, the fitter the mutant, the higher the probability to be chosen for reproduction. As a result, the greater the fitness of mutants is, the

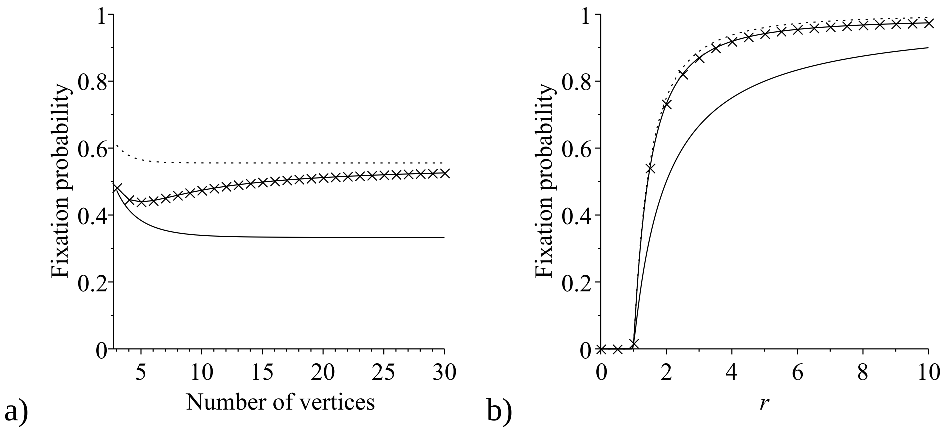


Figure 2.2: Comparison of the average fixation probability of a single mutant on a star graph (crosses) under the rules of the IP, with the approximation solution (1.38) (dotted line) and the fixation probability in the Moran process (1.33) (solid line), in the constant fitness case where (a) $r = 1.5$ and the number of vertices increases, (b) the number of vertices is equal to 60 and the fitness r increases.

higher their probability to fixate. In Figure 2.2b we observe the rapid increase in the fixation probability of mutants on both the star graph and in the Moran process as the fitness r varies from values less than 1 to values higher than 1. Especially for relatively large populations, the change in the fixation probability is almost a step change at $r = 1$.

The mean time to absorption starting from a single mutant

In this section, we consider the average required times to absorption starting from a single mutant on a star graph and compare with the times required on a circle and a complete graph.

As has been shown in Lieberman *et al.* (2005), the fixation probability of mutants introduced on any circulation graph (and thus on a complete graph and a circle) is equivalent to the fixation probability in the Moran process. However, in contrast to the fixation probability, considering the mean times to absorption and fixation we observe that different circulation graphs might yield significantly different absorption and fixation times. In our comparison between the circle and the complete graph we observe that absorption and mutant fixation is reached faster on the complete graph than the circle and as the population size increases, the speed to absorption and fixation decreases more on the circle. This is due to the fact that the number of mutant-mutant and resident-resident replacements before absorption is higher on the circle than on the complete graph. In addition, comparisons of the time before absorption and fixation occur on the circle and the compete graph with that on the

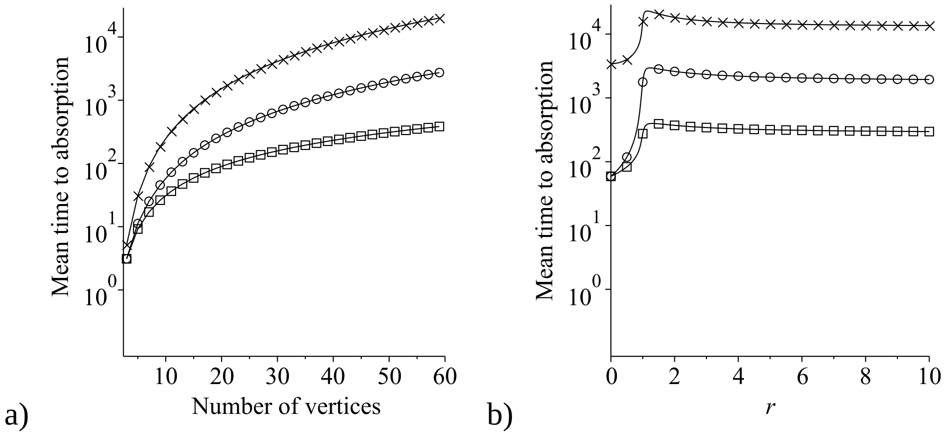


Figure 2.3: Comparison of the mean time to absorption starting from a single mutant on a star graph (crosses), a circle (circles) and a complete graph (boxes) under the rules of the IP, in the constant fitness case where (a) $r = 1.5$ and the number of vertices increases, (b) the number of vertices is equal to 60 and the fitness r increases.

star have shown that the absorption and fixation on the star is the slowest (see Figure 2.3). Hence, the advantage of the high probability that a mutant has to fixate on a star graph is accompanied by the disadvantage of the high times needed to absorption and fixation. Note that on a star, for large N, the first mutant is placed on a leaf with very high probability, thus a mutant placed on a leaf is quite safe, being killed at each time step with probability of the order of $1/N^2$; this increases the time needed for mutant elimination. For exactly the same reasons, even when all individuals but the last one (which is inevitably on a leaf) are mutants, at each time step the probability of mutant fixation is again of the order of $1/N^2$, which increases the time needed for mutants to fixate.

In Figure 2.3a it is observed that the increase of the population size increases the time to absorption in all structures, as expected. For constant population size, the mean time to absorption is an increasing function of $r \in (0, r_{\text{slowest}})$ and the time then decreases to a constant for $r > r_{\text{slowest}}$, in all three graphs. The constant corresponds to the number of steps needed for absorption given a mutant is selected for reproduction at every time step. Again, the limit is largest for the star (as there the mutant-mutant replacements are most frequent), followed by the circle and then by the complete graph. The value of r_{slowest} is different for different structures, but approaches 1 in each case as N increases. This means that absorption times are slowest in the case of neutral drift for large populations. This is because in this case individuals of the different types drift until an absorbing state is reached. For $r \approx 0$, on the circle and the complete graph the mean absorption time is around $N - 1$ (since a mutant never gives birth, and the probability that it is killed at each time step is $1/(N-1)$). However, on the star the mean absorption time is much larger, about

$((N-1)^3+1)/N$, since if the mutant is placed in the centre it is killed immediately, and otherwise it is killed at each step with probability $1/(N-1)^2$ (see Figure 2.3b).

For a more detailed consideration of the fixation probability and the times to absorption and fixation of a mutant on a star graph in the case of constant fitness, see Section 3.4.1.

The mean number of transitions before absorption occurs starting from a single mutant

In this section, we compare the effect of the three structures on the mean number of transitions before one of the two types of individuals reaches fixation, starting from a single mutant.

We first note that since on every circulation graph $p_{i,i-1}/p_{i,i+1} = 1/r$, as for the fixation probability (see Lieberman *et al.* (2005), Section 1.5), the mean number of transitions before absorption and mutants' fixation will be identical with that in the Moran process. Using the formula (1.34) with $p_{i,i+1} = \pi_{i,i+1} = r/(r+1)$ and $p_{i,i-1} = \pi_{i,i-1} = 1/(r+1)$, we obtain that the mean number of transitions before absorption starting from a single mutant A in a B resident population of size N in the Moran process, $\mathrm{M_M}$, is given by

$$\mathrm{M_M} = {}^{A}\mathrm{P_M} \sum_{j=1}^{N-1} (N-j) \left(\frac{r+1}{r^j} \right) = \frac{r^N - r^{N-1}}{r^N - 1} \sum_{j=1}^{N-1} (N-j) \left(\frac{r+1}{r^j} \right). \tag{2.128}$$

${}^{A}\mathrm{P_M}$ is the fixation probability of a single mutant A in the Moran process given by (1.33). Similarly, using (1.35), the mean number of transitions before As' fixation starting from a single A, ${}^{A}\mathrm{M_M}$, is found to be

$${}^{A}\mathrm{M_M} = \sum_{j=1}^{N-1} {}^{A}\mathrm{P}_{\mathrm{M}j} (N-j) \left(\frac{r+1}{r^j} \right) = \sum_{j=1}^{N-1} \frac{r^N - r^{N-j}}{r^N - 1} (N-j) \left(\frac{r+1}{r^j} \right), \tag{2.129}$$

where ${}^{A}\mathrm{P}_{\mathrm{M}j}$ is the fixation probability of j A individuals in the Moran process.

The increase of the population size increases the number of transitions until absorption in all structures. In particular, the number of transitions on the star increases much more than that in the Moran process, since the increase of the population size increases the chance of the first mutant being placed on a leaf. This results in the large number of replacements of the individual which occupies the central vertex by an individual of the other type before one of the two absorbing states is reached (see Figure 2.4a).

As for the absorption and fixation times, for constant population size, the in-

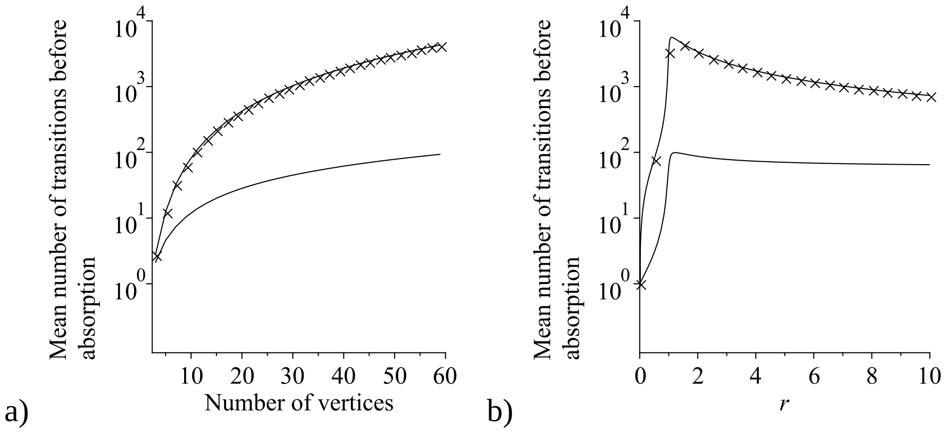


Figure 2.4: Comparison of the mean number of transitions until absorption starting from a single mutant on a star graph (crosses) under the rules of the IP, with the mean number of transitions in the Moran process, in the constant fitness case where (a) $r = 1.5$ and the number of vertices increases, (b) the number of vertices is equal to 60 and the fitness r increases.

crease of the fitness of disadvantageous mutants ($r < 1$) increases the mean number of transitions before one of the types of individuals in the population fixates, in all structures. In particular, the less the mutants' fitness, r, the faster the spread of resident individuals, and as r approaches zero, the number of transitions before residents fixation approaches 1, which is the transition where the first mutant is replaced by a resident. In each case, above a value of r which approaches one as the population size increases and at which the mean number of transitions reaches the maximum value, the fitter the mutants, the lower the mean number of transitions before their fixation. As the fitness of mutants becomes infinitely large, the mean number of transitions before absorption tends to the initial number of resident individuals ($N - 1$), in all structures, since then in each time step a resident individual is replaced by the offspring of a mutant (see Figure 2.4b).

2.6.2 The frequency dependent fitness case – The Hawk–Dove game played on graphs

In the previous example, we have assumed that the fitness of individuals is constant. However, in natural systems, the fitness of individuals depends on their interactions with other individuals of the population (see for examples, Maynard Smith and Price, 1973; Maynard Smith, 1982). In this section, we compare the fixation probability, the mean times to absorption and fixation and the mean number of transitions to absorption and fixation, when individuals use the strategies of a Hawk–Dove game (Maynard Smith and Price (1973); Maynard Smith (1982). See also Section 1.3.1) on a complete graph, a circle and a star graph.

The Hawk–Dove game is particularly interesting because in the infinite well-mixed population the evolutionary game dynamics yields a mixture of individuals playing Hawk or Dove.

The fixation probability of a mutant

On a star graph, a Dove has a higher fitness than a neighbouring Hawk in very few cases, moreover only in those where the fixation of the Hawk is already very likely (if N is not small). Indeed, if a Dove is in the center, then its fitness is no more than $f_b + wV/2$ while the fitness of a Hawk on a leaf is $f_b + wV$. If a Dove is on a leaf with a Hawk in the center, then the fitness of the Dove is equal to the background fitness, f_b, while the fitness of the Hawk ranges from $fb + wV$ (with no other Hawks in the population, i.e. when there is the highest danger of Hawk extinction), continuously going down to almost $f_b + w(V - C)/2$ (if there are Hawks on almost all other leaves, i.e. when Hawks are almost fixed in the population).

The increase of the cost C in relation with the value of the resource V, decreases the probability of Hawks being chosen for reproduction (when they interact with other Hawks) and thus their fixation probability on all of the three structures decreases as C increases (see Figure 2.5c and 2.5d). It is observed that the star yields the highest fixation probability for a single mutant Hawk compared to the other two structures (see Figure 2.5). On the star graph, it is shown that if the values of the payoffs are such that Hawks are favoured over Doves ($\rho_{\mathrm{IP}}^{\mathrm{S}} > 1$), then an increase of the population size increases the average fixation probability of a randomly placed mutant Hawk, ${}^{H}P$ (see Figure 2.5a). In this case, ${}^{H}P$ is found to approach $wV(3f_b + 2wV)/2(f_b + wV)^2$, and thus it becomes independent of the fight cost C (for a detailed consideration of the limits of the fixation probability of a single mutant on the star graph in various scenarios, see Chapter 3). This is because when there is a large number of mutant Hawks on the star, those on the leaves only play against the central individual, their fitness is independent of C when playing with a resident Dove in the central position and they are fitter than that Dove. If extinction happens it is very likely to happen early on (due to bad luck) when there are few Hawks, and in a large population if there are few Hawks the fitness of (the central) Hawk individuals does not depend much upon C. Thus, the increase of the population size decreases the effect of the cost, C. In contrast, on a circle or a complete graph, the increase in the population size yields lower fixation probability (see Figures 2.5a and 2.5b). Note that, in our example, for small N the expected pattern of declining fixation probability with population size happens on the star as well. On a

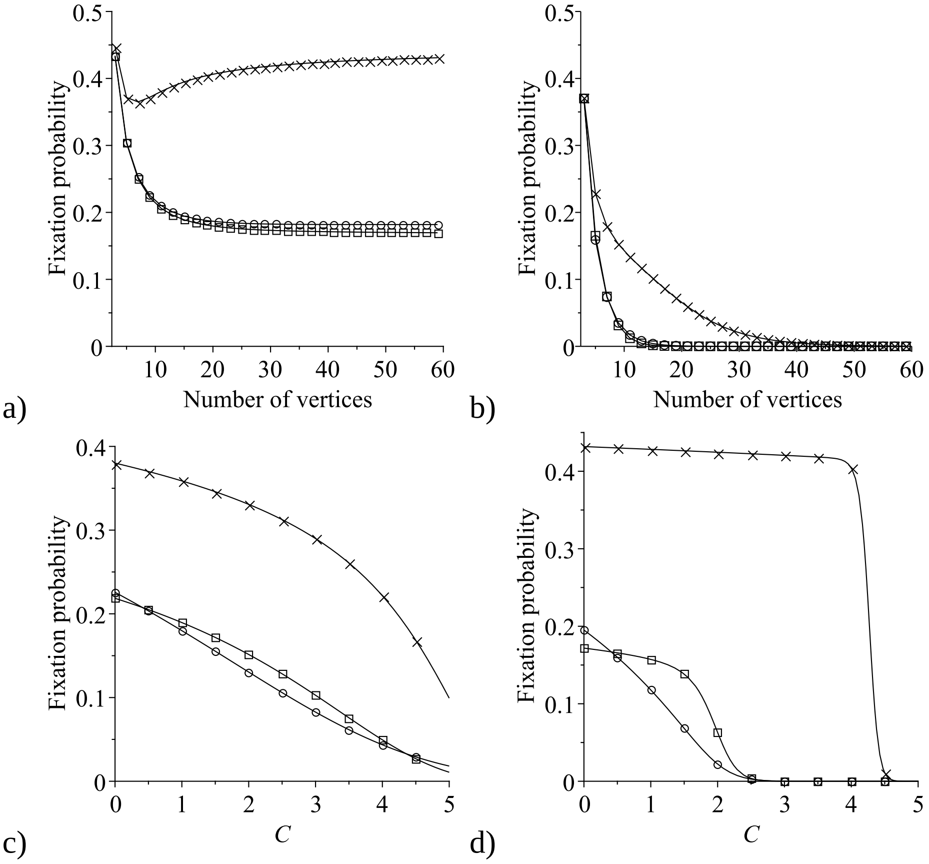


Figure 2.5: Comparison of the average fixation probability of a single mutant Hawk on a star graph (crosses), a circle (circles) and a complete graph (boxes) under the rules of the IP, in the Hawk–Dove game described by the payoff matrix (1.19) in the case where (a) $V = 1$ and $C = 0.2$, (b) $V = 1$ and $C = 4.7$, and the number of vertices varies, (c) the number of vertices is equal to 10, $V = 1$ and C varies, (d) the number of vertices is equal to 60, $V = 1$ and C varies. In all cases, $f_b = 2$ and $w = 1$.

large circle, if Hawks are favoured over Doves, i.e. if $C < 2V$ (see Section 2.5), then from the formula (2.76) we find that as the population size increases, ${}^{H}P$ decreases and approaches

$$
{}^{H}P \approx \frac{4w(f_b + wV)(2V - C)}{11(wV)^2 - 5w^2VC + 24f_bwV - 8f_bwC + 16f_b^2}. \tag{2.130}
$$

On a large complete graph, if the Hawk is the favoured strategy then ${}^{H}P$ approaches $wV/2(f_b + wV)$ with increasing population size. Therefore, in this case, as happens on a star graph, the larger the population size, the smaller the dependence of the fixation probability on the cost of the fight C. In the case where Dove is the favoured strategy ($\rho_{\text{IP}}^{\text{G}} < 1$), the increase of the population size reduces the fixation probability of Hawks rapidly to zero, in all structures (see Figure 2.5b). Especially on a large complete graph and a large star the fixation probability of Hawks is almost a step function with the step occurring when $\rho_{\mathrm{IP}}^{\mathrm{CG}} \approx 1$ and $\rho_{\mathrm{IP}}^{\mathrm{S}} \approx 1$, respectively (see Figure 2.5d).

Whether the fixation probability of Hawks is greater on the circle or on the complete graph depends on the values of V and C (see Figures 2.5c and 2.5d). When C is small, Hawks do better on the circle than on the complete graph. This is because even when the Hawk population is small, competing Hawks and Doves both gain their payoff from 50% Hawks and 50% Doves (given there are more than two Hawks and two Doves in the population), and this is advantageous to a Hawk when C is small, when compared to the well-mixed population case. When C is large, Hawks again do better on the circle. Here, the Hawk's chance of fixation in either case is low, and it needs good luck to reach a high proportion in the population. If this occurs, then on the complete graph it must achieve fixation with a payoff derived mainly from contests against Hawks, which will be low for large C, as opposed to the case on the circle, which is still from 50% Hawk and 50% Dove contests. It is also observed that the population size N is also very important in this comparison. Values of V and C which yield higher fixation probability on the circle than on the complete graph for small population size, might result in higher fixation probability on the complete graph for large population size.

The behaviour of the solution of the fixation probability of a single individual playing the Dove strategy when it is introduced into a population playing the Hawk strategy is almost symmetric on the three graphs. When the cost of the fight, C, and the payoff obtained when the fight is won, V, are such that all the graphs favour the evolution of the Hawk strategy over the Dove strategy, then the star is the worst graph for Doves with respect to their probability of fixation, followed either by the circle or the complete graph, depending on the values of V and C, and the population size (see Figure 2.6a). In this case, the increase of the population size reduces the fixation probability of Doves to zero, in all structures. Whenever C is high compared to V such that the Dove strategy is favoured over the Hawk strategy on all the three graphs we consider, the numerical examples indicate that the chance of Doves to fixate is higher on the complete graph followed by that on either the star or the circle, depending on the size of the population. In this case, the advantage of Doves with respect to their fixation probability on both the complete graph and the star increases with the increasing population size (if the population is not too small) while that of the circle decreases (see Figure 2.6b). As one could expect, the greater the value of the cost C, i.e. the less the chance of Hawks to be chosen for reproduction when connected to other Hawks, the higher the probability of Doves to take over a population of Hawks in all structures (see Figures 2.6c and 2.6d). Especially in large popula-

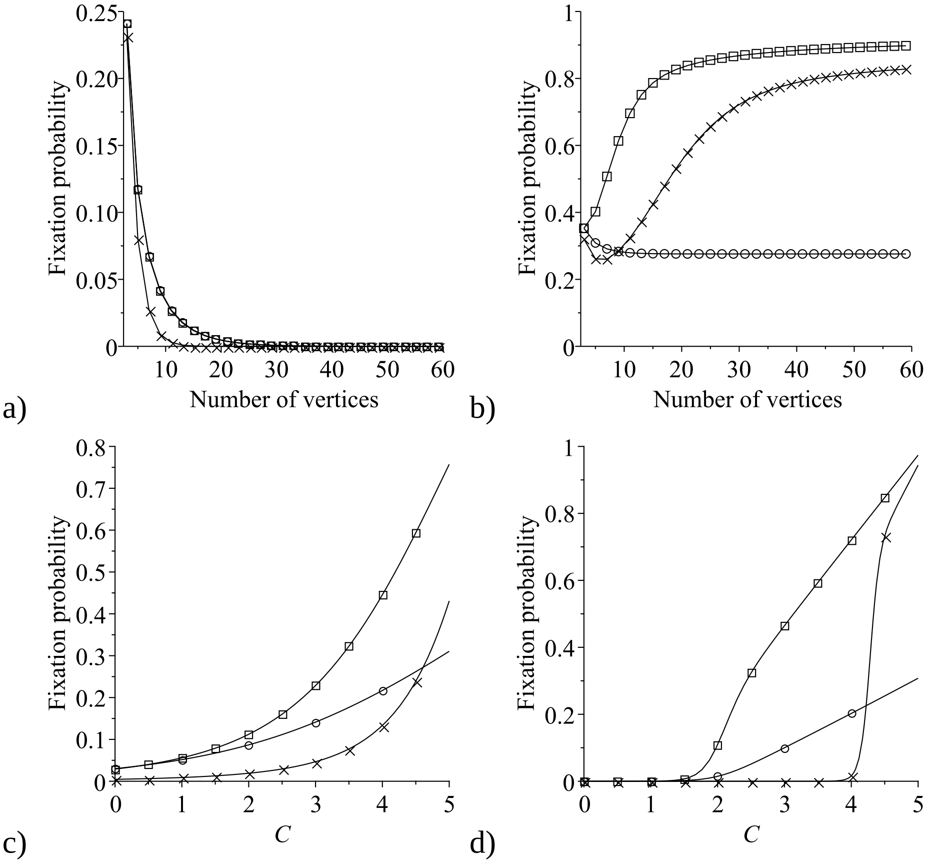


Figure 2.6: Comparison of the average fixation probability of a single mutant Dove on a star graph (crosses), a circle (circles) and a complete graph (boxes) under the rules of the IP, in the Hawk–Dove game described by the payoff matrix (1.19) in the case where (a) $V = 1$ and $C = 0.2$, (b) $V = 1$ and $C = 4.7$, and the number of vertices varies, (c) the number of vertices is equal to 10, $V = 1$ and C varies, (d) the number of vertices is equal to 60, $V = 1$ and C varies. In all cases, $f_b = 2$ and $w = 1$.

tions, once C increases to values such that the Dove strategy becomes the favoured strategy, then a rapid increase in the fixation probability of Doves occurs.

Mean time to absorption starting from a single mutant

As already mentioned in the example of the constant fitness case, the increase of the population size increases the mean time to absorption in all structures. Depending on the values of C, this increase might be much higher on the star (see Figures 2.7 and 2.8). Our numerical examples suggest that the star always yields the highest absorption time, while depending on the values of V, C and the population size, absorption is reached faster either on the complete graph or on the circle.

On the complete graph and the star graph, since the probability of a Hawk's reproduction decreases with the increase of C (when it interacts with at least one other Hawk), the time to Hawks' fixation increases in increasing C. On the other hand,

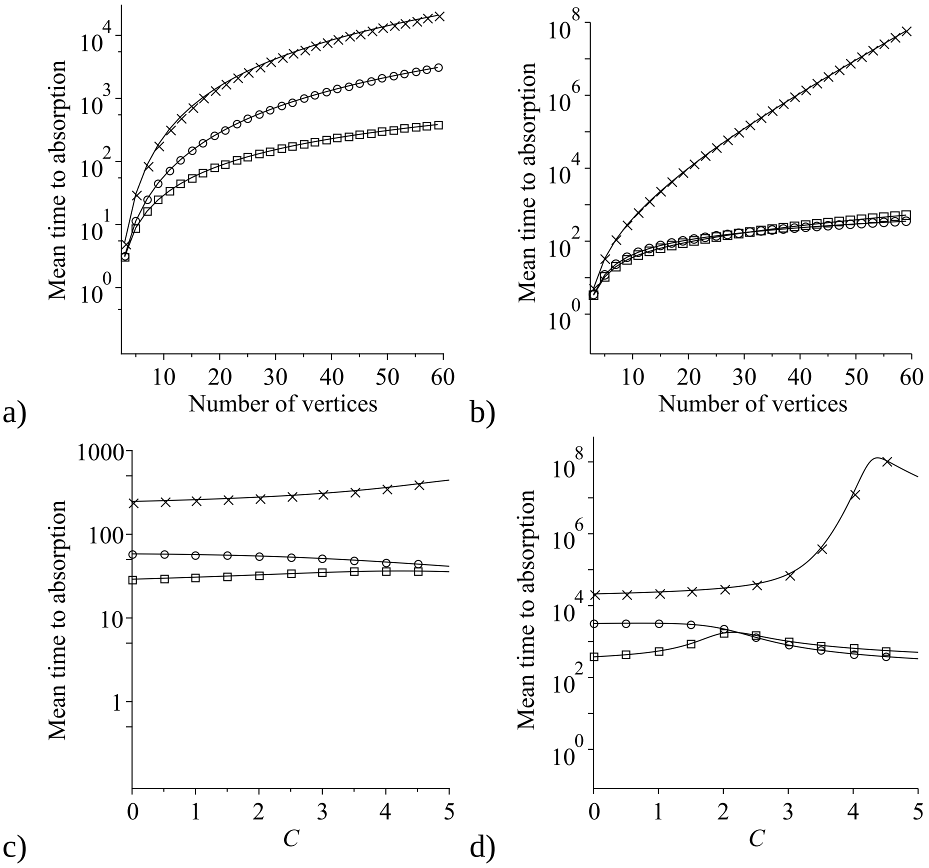


Figure 2.7: Comparison of the mean time to absorption starting from a single mutant Hawk on a star graph (crosses), a circle (circles) and a complete graph (boxes) under the rules of the IP, in the Hawk–Dove game described by the payoff matrix (1.19) in the case where (a) $V = 1$ and $C = 0.2$, (b) $V = 1$ and $C = 4.7$, and the number of vertices varies, (c) the number of vertices is equal to 10, $V = 1$ and C varies, (d) the number of vertices is equal to 60, $V = 1$ and C varies. In all cases, $f_b = 2$ and $w = 1$.

since C matters only when there are enough Hawks in the population, the change of C does not much affect the time of Hawks being eliminated (especially at the beginning of the invasion). Consequently, for small N, the mean time to absorption increases with the increase of C (see Figure 2.7c). When N is large, there is a certain tendency for the number of Hawks to stabilise around the internal equilibrium point of the stochastic process. However, the extinction of either Hawks or Doves is inevitable and the evolutionary process ends at absorption due to stochasticity in a finite population, as opposed to the result of evolutionary pressure. Hence, on each of the complete graph and the star the process takes the most time when the average fixation probability of a single Hawk is equal to the average fixation probability of a single Dove, i.e. when $\rho_{\mathrm{IP}}^{\mathrm{CG}} \approx 1$ and $\rho_{\mathrm{IP}}^{\mathrm{S}} \approx 1$, respectively (see Figure 2.7d).

On the circle, when a single Hawk is introduced into a population of Doves, in small populations, although a decrease in the absorption time is observed as C

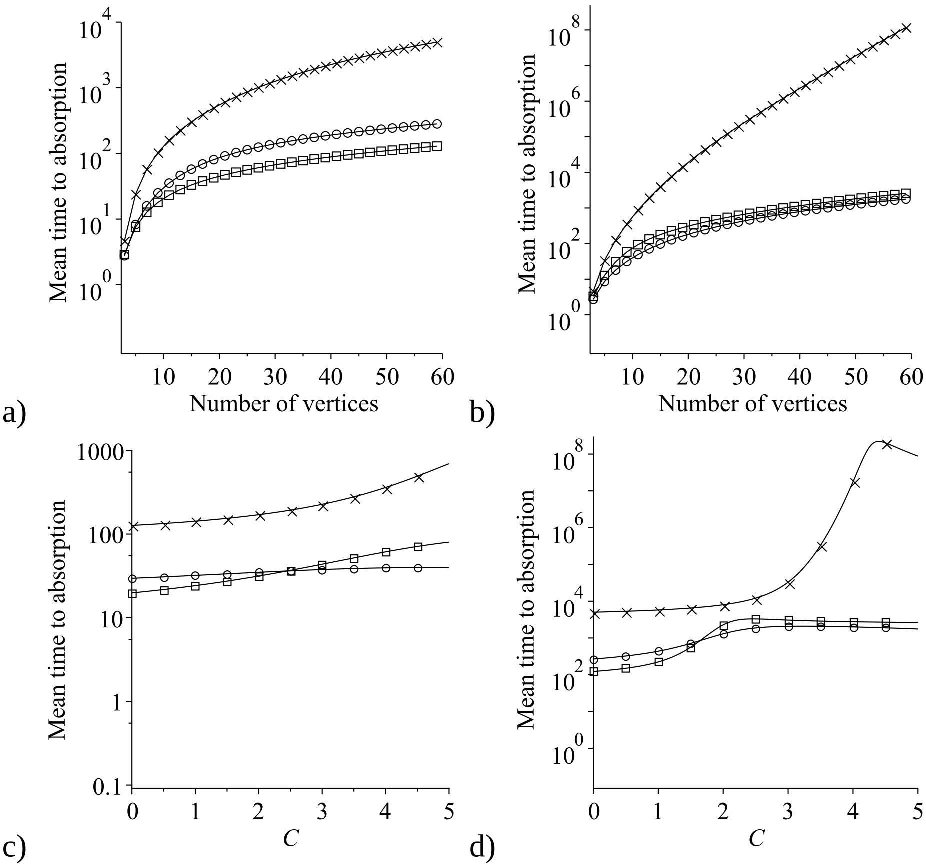


Figure 2.8: Comparison of the mean time to absorption starting from a single mutant Dove on a star graph (crosses), a circle (circles) and a complete graph (boxes) under the rules of the IP, in the Hawk–Dove game described by the payoff matrix (1.19) in the case where (a) $V = 1$ and $C = 0.2$, (b) $V = 1$ and $C = 4.7$, and the number of vertices varies, (c) the number of vertices is equal to 10, $V = 1$ and C varies, (d) the number of vertices is equal to 60, $V = 1$ and C varies. In all cases, $f_b = 2$ and $w = 1$.

increases, this is not significant since absorption occurs relatively fast. However, in very large populations there is a pronounced decrease of the mean time to absorption when C becomes higher than $2V$. This is because, when $C > 2V$, a Dove on the boundary between two segments, one consisting of more than one Hawk and one consisting of more than one Dove, becomes fitter than a neighbouring Hawk and thus Hawks are more likely to go extinct in significantly less time (see Figure 2.7).

A symmetric situation occurs when in a population of Hawks a single individual uses the Dove strategy. When C increases compared to V, the Hawks lose their advantage and it thus takes longer to eliminate Doves. When C increases above the value at which $C \approx 2V$, then on a large circle there is a significant increase of the absorption time, since in this case, a single Dove spreads in the population playing the Hawk strategy and eventually fixates (see Figure 2.8).

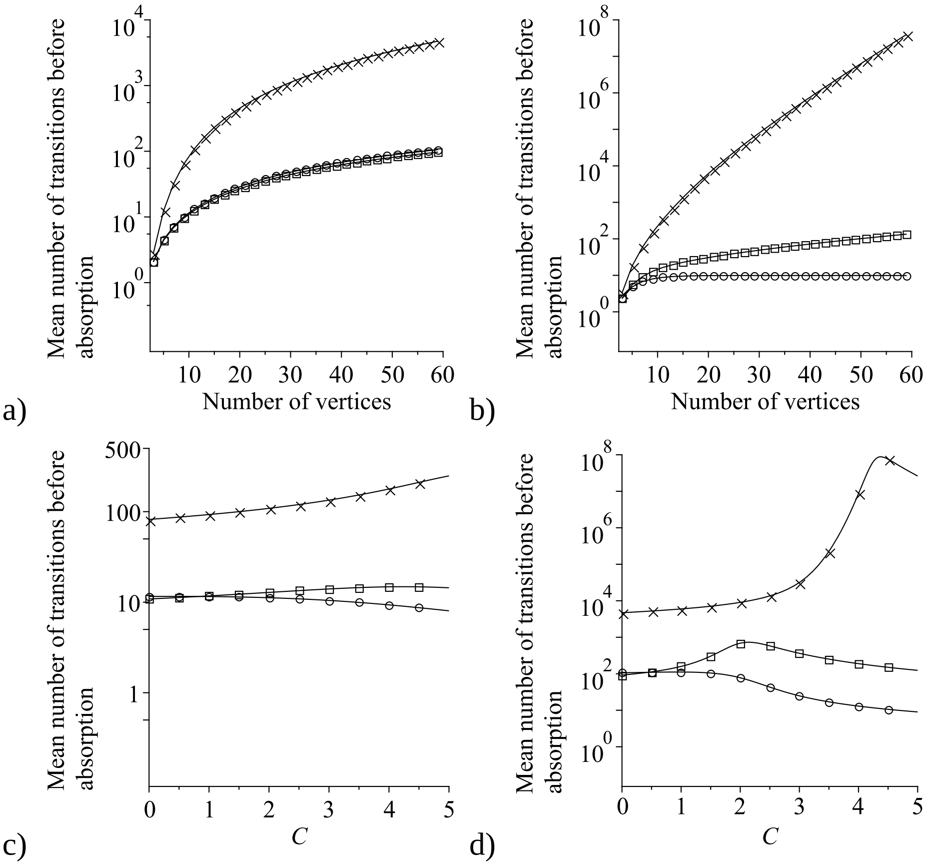


Figure 2.9: Comparison of the mean number of transitions until absorption starting from a single mutant Hawk on a star graph (crosses), a circle (circles) and a complete graph (boxes) under the rules of the IP, in the Hawk–Dove game described by the payoff matrix (1.19) in the case where (a) $V = 1$ and $C = 0.2$, (b) $V = 1$ and $C = 4.7$, and the number of vertices varies, (c) the number of vertices is equal to 10, $V = 1$ and C varies, (d) the number of vertices is equal to 60, $V = 1$ and C varies. In all cases, $f_b = 2$ and $w = 1$.

The mean number of transitions before absorption occurs

Here, through numerical examples we compare the mean number of transitions to absorption on the three different structures. We present examples in the cases where a single individual playing one strategy invades into a population playing the other in a Hawk–Dove game (see Figures 2.9 and 2.10). In this evolutionary dynamics, the behaviour of the solutions of the mean number of transitions before absorption and fixation are similar to the behaviour of the solutions of the mean time to absorption and fixation. Clearly, the mean number of transitions before the fixation of either strategy is lower than the respective time to fixation, apart from some extreme cases where the two quantities can be equal.

As we have seen in the constant fitness case, the mean number of transitions before absorption increases as the population size increases, with the increase on the star to be much larger than that on a circle and a complete graph, especially when

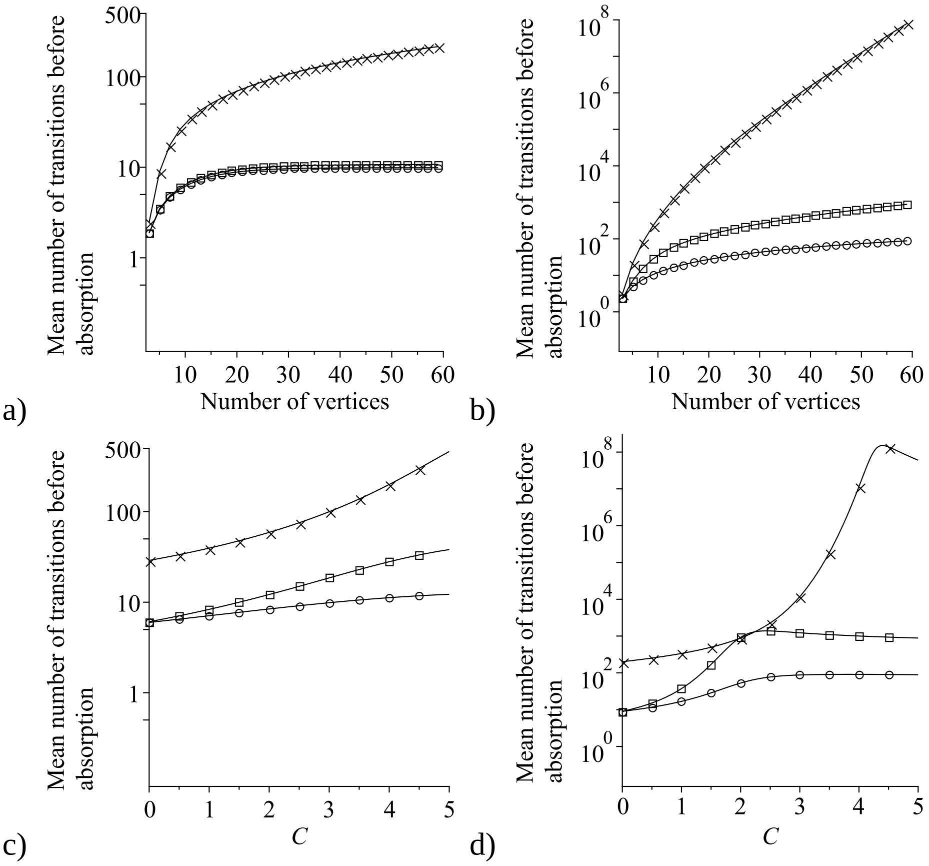


Figure 2.10: Comparison of the mean number of transitions until absorption starting from a single mutant Dove on a star graph (crosses), a circle (circles) and a complete graph (boxes) under the rules of the IP, in the Hawk–Dove game described by the payoff matrix (1.19) in the case where (a) $V = 1$ and $C = 0.2$, (b) $V = 1$ and $C = 4.7$, and the number of vertices varies, (c) the number of vertices is equal to 10, $V = 1$ and C varies, (d) the number of vertices is equal to 60, $V = 1$ and C varies. In all cases, $f_b = 2$ and $w = 1$.

the cost of playing Hawk against a Hawk is very high (due to the high number of transitions before Hawks take over the entire population and fixate).

Note that as for the fixation probability, the mean number of transitions is no longer identical on all circulation graphs in the frequency dependent fitness case. Here, depending on the values of the payoffs and the population size, the mean number of transitions before absorption is either greater on the circle or on the complete graph.

In addition, although in our examples, especially those in Figures 2.7c and 2.7d, the mean time to absorption in most of the cases is higher when individuals are placed on a circle than when they are placed on a complete graph, the mean number of transitions before absorption is higher on the complete graph. This verifies that absorption on the circle is usually reached slower than on the complete graph due to larger number of replacements between individuals of the same type.

2.7 Discussion

In this chapter, we have studied analytically the stochastic evolutionary game dynamics in finite structured populations represented by three simple graphs; a complete graph, a circle and a star graph. We first derived the exact solutions of the fixation probability, the mean absorption time, the mean fixation time as well as the mean number of transitions before absorption and mutants' fixation occur, starting from any number of mutant individuals introduced into the three graphs. Using these results we have obtained conditions under which the mutant strategy is favoured over the population strategy. The solutions are general and can be applied to stochastic evolutionary processes where in each time step there is one birth and one death event and there is no mutation, just selection. We have applied the results in the IP and, through numerical investigation, we have considered the effect of the three population structures on the above quantities when a single mutant individual invades into a resident population. We have first studied the case where the fitness of individuals does not depend on the interactions with neighbouring individuals but remains constant. We have then adapted the classical Hawk–Dove game to evolution on graphs.

In the constant fitness case, an advantageous mutant has always a higher probability to fixate on the star than on a circulation graph, such as a complete graph and a circle, where the fixation probability is equal to the fixation probability in the Moran process. Similarly, a disadvantageous mutant has a lower chance to fixate on the star. Thus, the star graph acts as an amplifier of the fitness and enhances selection. However, the star graph costs to mutants a very long time before their fixation. We have also demonstrated that although the fixation probability on the complete graph and the circle (and every circulation graph) is identical with the fixation probability in the Moran process, the absorption and fixation times are different. The complete graph is the quickest of the three graphs for mutant individuals and the star the slowest. For large population size, for each graph, times are longest in the case of neutral drift, where mutants' fitness is identical to that of residents.

Applying the Hawk–Dove game we have seen that there is not a consistent relationship between the three graphs regarding which gives the highest mutant fixation probability and the fastest time to absorption and fixation, since this depends on the cost of the fight C and the payoff of the win V. The size of the population is also very important in such comparisons as a strategy might does better on one graph than on other graphs in populations of small size but worse in larger populations. In addition, even on a specific graph, a strategy might be favoured over the other strategy for small population sizes but not for large population sizes. However, there are certainly features of interest. For example, on the complete graph and the star we observe that values of C and V such that $\rho^{\mathrm{G}}_{\mathrm{IP}} \approx 1$ yield very slow fixation times for large population sizes, as selection pressure favours the mixture of the two strategies. Thus the two strategies coexist for a long time before the extinction of one of the two strategies, an inevitable event due to the finiteness of the population. Indeed, it would be of interest to consider the quasi-stationary distribution of such a population, conditional on such extinctions not occurring (this may resemble more accurately the results of simulations, for instance). For such values of C and V there is also a step change in the fixation probability of a single Hawk, with a significant non-zero probability for $\rho^{\mathrm{G}}_{\mathrm{IP}} > 1$, and a near zero value otherwise. Hence, although the detailed consideration of the absorption and fixation time is particularly novel, it is demonstrated that this is a significant quantity for the description of the evolutionary process, especially in cases where evolution favours the coexistence of strategies, as the fixation probability itself in such cases is not sufficient to describe the evolution of the system. The circle, which is another regular graph, exhibits different behaviour. As on the complete graph and the star, when C and V take values such that $\rho^{\mathrm{C}}_{\mathrm{IP}} < 1$, the fixation probability of a single Hawk decreases rapidly to zero, while a significant decrease of the absorption and fixation time also occurs. An interesting relationship between the circle and the complete graph is observed, where low and high values of C, compared to V, give higher fixation probabilities on the circle than the complete graph, with intermediate values higher on the complete graph.

The structure of the population can significantly affect the outcome of the evolutionary process. It has been shown that the magnitude of this effect depends on the population size and the fitness of individuals. Another interesting factor that might influence the evolutionary process is the update rules of the evolutionary dynamics. In the next chapter, we investigate the impact that the strategy update rules might have on the evolution of a population by considering the evolutionary process on the extreme structure of the star graph under various update rules.

CHAPTER 3

Evolutionary dynamics on graphs under various update rules

3.1 Introduction

In Chapter 2, it has been shown the significant role that the population structure might play in the evolutionary process following the update rules of the invasion process (IP). Moreover, there are a number of update rules that can be followed. This has not been of great importance historically, since the evolutionary process on homogeneous populations is not significantly affected by the choice of the update rules. However, recent studies suggest that different update rules might result in significant differences in the evolutionary process in populations with a non-homogeneous structure (for example, Antal *et al*., 2006; Sood *et al*., 2008; Masuda, 2009). In this chapter we consider analytically the stochastic evolutionary process following four commonly used update rules on the simplest heterogeneous graph, the star graph.

The fitness of each individual f, as in Section 2.4, is assumed to be $f = f_b + wP$, where f_b is the constant background fitness of every individual, P is the average of the payoffs obtained by the games played against all the neighbouring connected individuals and $w \in [0, \infty)$ represents the intensity of selection.

We assume a certain number of individuals playing a strategy X is introduced into a finite population of individuals playing a strategy Y. Due to the finiteness of the population, through evolution the population will eventually reach a state where all individuals play the same strategy. For four different update rules, we investigate the fixation probability and the mean absorption and fixation times (see Section 1.4), when the individuals of the population are placed on a star graph, starting from any population composition.

In Section 3.2 we first present the update rules we will consider and the transition probabilities under each of them on the star graph. The transition probabilities under the different update rules on the circle and the complete graph are also presented. In Section 3.3, for each of the update rules we derive the appropriate conditions under which one strategy is favoured over the other. In Section 3.4, we apply our results to two specific cases; the case where individuals have constant fitness, and the frequency dependent fitness case where the fitness of individuals depends on the interactions with the different types of neighbouring individuals. In the latter case, we study three example games; the Hawk–Dove game, the Prisoner's Dilemma and coordination games.

3.2 Evolutionary games on star graphs under various update rules

3.2.1 Update rules – Transition probabilities

In Chapter 2, the evolutionary process on the star has been considered analytically under the update rules of the IP. Here, we consider three update rules additional to the IP; *the birth-death process with selection on the death* (BD-D), the *biased voter model* (VM) (or death-birth process with selection on the death) and the *death-birth process with selection on the birth* (DB-B).

Consider a game between two strategies, A and B, interacting on a star graph with n leaves. The game played is described by the payoff matrix (1.2).

The BD-D process (Masuda, 2009) is a process where at each time step an individual is chosen for reproduction at random and then its offspring replaces a neighbouring individual which is chosen with probability inversely proportional to its fitness for death. Thus, in this process, the number of A individuals on the leaves of the star increases (decreases) by one if an A (a B) individual placed in the center is chosen for reproduction at random, with probability $1/(n+1)$, and its offspring replaces a B (an A) individual on the leaves which is chosen inversely proportional to its fitness. Thus, the fitness of the individual in the centre in this case is irrelevant. The individual in the centre is replaced by the offspring of an individual of the other type whenever an individual of the other type is chosen randomly for reproduction, and thus irrespective of the fitness of individuals. The transition probabilities from one state to another under this process are

$$p^{AA}_{i,i+1} = \frac{1}{n+1}\cdot\frac{\frac{1}{\gamma}(n-i)}{i\frac{1}{\alpha}+(n-i)\frac{1}{\gamma}} = \frac{(n-i)\alpha}{(n+1)\big(i\gamma+(n-i)\alpha\big)}, \tag{3.1}$$

$$p^{AB}_{i,i} = \frac{n-i}{n+1}, \tag{3.2}$$

$$p^{BB}_{i,i-1} = \frac{1}{n+1}\cdot\frac{\frac{1}{\beta}i}{i\frac{1}{\beta}+(n-i)\frac{1}{\delta}} = \frac{i\delta}{(n+1)\big(i\delta+(n-i)\beta\big)}, \tag{3.3}$$

$$p^{BA}_{i,i} = \frac{i}{n+1}, \tag{3.4}$$

and zero in any other case. $p^{AA}_{i,i} = 1 - p^{AA}_{i,i+1} - p^{AB}_{i,i}$ and $p^{BB}_{i,i} = 1 - p^{BB}_{i,i-1} - p^{BA}_{i,i}$, $\forall\ i \in [0,n]$. We recall that $p^{XY}_{i,j}$ denotes the transition probability from a state with i A individuals on the leaves and an X individual in the center to the state with j A individuals on the leaves and a Y individual in the center (see Section 2.3). $\alpha = f_b + wa$, $\beta = f_b + wb$, $\gamma = f_b + wc$ and $\delta = f_b + wd$.

In the VM (Antal *et al.*, 2006), an individual first dies with probability inversely proportional to its fitness, and thus fitter individuals are more likely to survive, and is then replaced by the offspring of a randomly chosen neighbour. In this process, the number of A individuals on the leaves increases (decreases) by one given an A (a B) individual is placed in the centre, whenever a B (an A) individual on the leaves is chosen for death, since in this case the individual in the centre will inevitably reproduce and its offspring will replace the dead individual. The individual in the centre is replaced by an individual of the other type whenever it is chosen for death and a random individual of the other type on the leaves for reproduction. Thus, the non-zero transition probabilities are

$$p^{AA}_{i,i+1} = \frac{\frac{1}{\gamma}(n-i)}{\frac{1}{f_{Ac}(i)}+i\frac{1}{\alpha}+(n-i)\frac{1}{\gamma}} = \frac{(n-i)\big(i\alpha+(n-i)\beta\big)\alpha}{n\alpha\gamma+\big(i\alpha+(n-i)\beta\big)\big(i\gamma+(n-i)\alpha\big)}, \tag{3.5}$$

$$p^{AB}_{i,i} = \frac{\frac{1}{f_{Ac}(i)}}{\frac{1}{f_{Ac}(i)}+i\frac{1}{\alpha}+(n-i)\frac{1}{\gamma}}\cdot\frac{n-i}{n} = \frac{(n-i)\alpha\gamma}{n\alpha\gamma+\big(i\alpha+(n-i)\beta\big)\big(i\gamma+(n-i)\alpha\big)}, \tag{3.6}$$

$$p^{BB}_{i,i-1} = \frac{\frac{1}{\beta}i}{\frac{1}{f_{Bc}(i)}+i\frac{1}{\beta}+(n-i)\frac{1}{\delta}} = \frac{i\delta\big(i\gamma+(n-i)\delta\big)}{n\beta\delta+\big(i\gamma+(n-i)\delta\big)\big(i\delta+(n-i)\beta\big)}, \tag{3.7}$$

$$p^{BA}_{i,i} = \frac{\frac{1}{f_{Bc}(i)}}{\frac{1}{f_{Bc}(i)}+i\frac{1}{\beta}+(n-i)\frac{1}{\delta}}\cdot\frac{i}{n} = \frac{i\beta\delta}{n\beta\delta+\big(i\gamma+(n-i)\delta\big)\big(i\delta+(n-i)\beta\big)}. \tag{3.8}$$

$p^{AA}_{i,i} = 1 - p^{AA}_{i,i+1} - p^{AB}_{i,i}$ and $p^{BB}_{i,i} = 1 - p^{BB}_{i,i-1} - p^{BA}_{i,i}$, $\forall\ i \in [0,n]$. Recall that $f_{Ac}(i)$

$(f_{Bc}(i))$ is the fitness of an A (a B) individual placed in the centre of a star with i As and $n-i$ Bs on the leaves (see Section 2.4.3).

In the DB-B process (Ohtsuki *et al.*, 2006), in each time step an individual dies at random. Then, the gap is occupied by the offspring of a neighbouring individual chosen with probability proportional to its fitness. In cultural evolution and learning on social networks, this process can also be described as follows: a random individual is chosen to update its strategy (or idea, opinion, etc.) and adopts one of its neighbours' strategies proportional to their fitness. In this process, the number of A individuals on the leaves increases (decreases) by one, given an A (a B) individual is in the centre, whenever a B (an A) individual on the leaves is chosen to die at random. Thus, the increase (decrease) of individuals on the leaves is unaffected by the fitness of individuals. An individual in the centre is replaced by an individual of the other type if it is chosen for death at random, with probability $1/(n+1)$, and is replaced by the offspring of an individual of the other type, which is chosen for reproduction from among the individuals on the leaves with probability proportional to its fitness. Thus, the probabilities of moving from one state to another in this process are given by

$$p^{AA}_{i,i+1} = \frac{n-i}{n+1}, \tag{3.9}$$

$$p^{AB}_{i,i} = \frac{1}{n+1}\cdot\frac{\gamma(n-i)}{i\alpha+(n-i)\gamma} = \frac{(n-i)\gamma}{(n+1)\big(i\alpha+(n-i)\gamma\big)}, \tag{3.10}$$

$$p^{BB}_{i,i-1} = \frac{i}{n+1}, \tag{3.11}$$

$$p^{BA}_{i,i} = \frac{1}{n+1}\cdot\frac{\beta i}{i\beta+(n-i)\delta} = \frac{i\beta}{(n+1)\big(i\beta+(n-i)\delta\big)}. \tag{3.12}$$

and zero in any other case. $p^{AA}_{i,i} = 1 - p^{AA}_{i,i+1} - p^{AB}_{i,i}$ and $p^{BB}_{i,i} = 1 - p^{BB}_{i,i-1} - p^{BA}_{i,i}$, $\forall$ $i \in [0,n]$.

We observe that for $a=c$ and $b=d$ the BD-D and DB-B processes are equivalent to the respective cases of neutral drift, because then an A and a B individual on the leaves have equal fitness when playing against either an A or a B individual in the centre, and the central individual is selected at random irrespective of its fitness.

In all processes, at every time step an individual gives birth and an individual dies. Thus, the population size remains constant. As in the IP, it is assumed that in the evolutionary processes there is no mutation, just selection. It should also be noted that to be meaningful in the context of all of the above stochastic dynamics, since the transition probabilities from one state to another are proportional or inversely proportional to fitness, the fitness of each individual has to be non-negative (in some cases strictly positive), and we assume this throughout this work.

Surprisingly, we observe that for $b = c$, the conditional transition probabilities (2.7)–(2.8) are equal in the VM and the DB-B process. Thus, in this case the fixation probabilities of any number of mutants placed at any position on the star are equal in the two processes, irrespective of what the population size and the elements of the payoff matrix are.

For informational reasons, in Appendix B.1 we also present the transition probabilities on the circle under the three additional update rules. The fixation probability, the absorption and fixation times as well as the mean number of transitions before absorption and fixation on the circle under the different update rules can be considered by using the formulae derived in Chapter 2. The evolutionary process on the circle under different update rules has also been studied in Ohtsuki and Nowak (2006a).

On a complete graph of finite size N, the transition probabilities under the IP have been derived in Section 2.4.1.

Following the update rules of the BD-D process described above, the transition probabilities on the complete graph are given by

$$\begin{aligned}
p_{i,i+1} &= \frac{i}{N} \cdot \frac{\frac{1}{f_B}(N-i)}{(i-1)\frac{1}{f_A} + (N-i)\frac{1}{f_B}} \\
&= \frac{i}{N} \cdot \frac{(N-i)\big((i-1)\alpha + (N-i)\beta\big)}{(N-i)\big((i-1)\alpha + (N-i)\beta\big) + (i-1)\big(i\gamma + (N-i-1)\delta\big)}, \qquad (3.13)\\
p_{i,i-1} &= \frac{N-i}{N} \cdot \frac{\frac{1}{f_A} i}{i\frac{1}{f_A} + (N-i-1)\frac{1}{f_B}} \\
&= \frac{N-i}{N} \cdot \frac{i\big(i\gamma + (N-i-1)\delta\big)}{(N-i-1)\big((i-1)\alpha + (N-i)\beta\big) + i\big(i\gamma + (N-i-1)\delta\big)}, \qquad (3.14)
\end{aligned}$$

where $f_A = f_b + wP_A$ ($f_B = f_b + wP_B$) is the fitness of an A (a B) individual on the complete graph. The payoffs P_A and P_B are given by (2.61)–(2.62).

In the VM, the transition probabilities on the complete graph are

$$\begin{aligned}
p_{i,i+1} &= \frac{(N-i)\frac{1}{f_B}}{i\frac{1}{f_A} + (N-i)\frac{1}{f_B}} \cdot \frac{i}{N-1} \\
&= \frac{(N-i)\big((i-1)\alpha + (N-i)\beta\big)}{(N-i)\big((i-1)\alpha + (N-i)\beta\big) + i\big(i\gamma + (N-i-1)\delta\big)} \cdot \frac{i}{N-1}, \qquad (3.15)
\end{aligned}$$

$$\begin{aligned} p_{i,i-1} &= \frac{i\frac{1}{f_A}}{i\frac{1}{f_A}+(N-i)\frac{1}{f_B}}\cdot\frac{N-i}{N-1} \\ &= \frac{i\big(i\gamma+(N-i-1)\delta\big)}{(N-i)\big((i-1)\alpha+(N-i)\beta\big)+i\big(i\gamma+(N-i-1)\delta\big)}\cdot\frac{N-i}{N-1}. \end{aligned} \tag{3.16}$$

In the DB-B process, the transition probabilities are given by

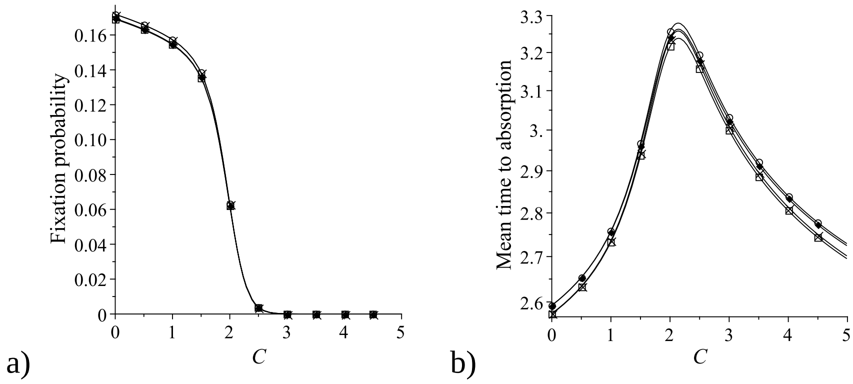
$$\begin{aligned} p_{i,i+1} &= \frac{N-i}{N}\cdot\frac{i f_A}{i f_A+(N-i-1) f_B} \\ &= \frac{N-i}{N}\cdot\frac{i\big((i-1)\alpha+(N-i)\beta\big)}{i\big((i-1)\alpha+(N-i)\beta\big)+(N-i-1)\big(i\gamma+(N-i-1)\delta\big)}, \end{aligned} \tag{3.17}$$

$$\begin{aligned} p_{i,i-1} &= \frac{i}{N}\cdot\frac{(N-i) f_B}{(i-1) f_A+(N-i) f_B} \\ &= \frac{i}{N}\cdot\frac{(N-i)\big(i\gamma+(N-i-1)\delta\big)}{(i-1)\big((i-1)\alpha+(N-i)\beta\big)+(N-i)\big(i\gamma+(N-i-1)\delta\big)}. \end{aligned} \tag{3.18}$$

The detailed consideration of the evolutionary process on the complete graph under different update rules is of less interest, especially when the population size is relatively large. Figure 3.1 shows the fixation probability and the mean time to absorption of a single Hawk in a Hawk–Dove game, described by the payoff matrix (1.19), as the cost C varies. It is observed that mutants have almost the same probability to fixate under the different dynamics (especially in large populations) with those in the IP and the VM being identical. In general, it is shown that the fixation probability of any number of mutants under these two processes is identical on all regular graphs of the same size for all games (Antal *et al.*, 2006; Sood *et al.*, 2008). The mean time needed for the system to reach absorption and mutant fixation is also almost independent of the choice of the update rule.

3.3 Favoured strategies on a star graph under various update rules

In this section, we present the appropriate conditions under which one of the strategies, A or B, is favoured over the other, i.e. the conditions where the fixation probability of a single individual playing the one strategy X in a population of individuals playing the other strategy Y, ${}^{X}P$, is higher than the fixation probability of a single individual playing Y in a population of individuals playing X, ${}^{Y}P$. Hence, we seek conditions on $\rho^{\mathrm{S}}_{\mathrm{UR}} \gtreqless 1$ (see section 2.5). We recall that $\rho^{\mathrm{G}}_{\mathrm{UR}}$ is defined as the ratio ${}^{X}P/{}^{Y}P$ on a graph G under the update rule UR. The analytic derivation of the con-



a) b)

Figure 3.1: (a) The fixation probability of Hawks, and (b) the mean time to absorption, starting from a single mutant Hawk on a complete graph with $N = 60$ vertices under the IP (crosses), the BD-D process (diamonds), the VM (circles) and the DB-B process (boxes), in the Hawk–Dove game described by the payoff matrix (1.19) as the fight cost, C, varies. $V = 1$, $f_b = 2$ and $w = 1$.

ditions is shown in the Appendix B.2. The respective condition in the IP has been derived in Section 2.5.

In the BD-D process, for large n we find (see Appendix B.2.2)

$$\rho^{\mathrm{S}}_{\text{BD-D}} \gtrless 1 \Leftrightarrow \left(\frac{\delta}{\beta}\right)^{\frac{\beta}{\delta-\beta}} \gtrless \left(\frac{\alpha}{\gamma}\right)^{\frac{\gamma}{\alpha-\gamma}}, \quad \alpha \neq \gamma,\ \beta \neq \delta. \tag{3.19}$$

In the VM, for large n we find (see Appendix B.2.3)

$$\rho^{\mathrm{S}}_{\text{VM}} \gtrless 1 \Leftrightarrow \alpha(\beta+\delta)\left(\frac{\alpha}{\beta}\right)^{\frac{\gamma}{\beta-\alpha}} \gtrless \delta(\gamma+\alpha)\left(\frac{\delta}{\gamma}\right)^{\frac{\beta}{\gamma-\delta}}, \quad \alpha \neq \beta,\ \gamma \neq \delta. \tag{3.20}$$

In the DB-B process for large n we find (see Appendix B.2.4)

$$\rho^{\mathrm{S}}_{\text{DB-B}} \gtrless 1 \Leftrightarrow \alpha(\beta+\delta)\left(\frac{\alpha}{\gamma}\right)^{\frac{\gamma}{\gamma-\alpha}} \gtrless \delta(\gamma+\alpha)\left(\frac{\delta}{\beta}\right)^{\frac{\beta}{\beta-\delta}}, \quad \alpha \neq \gamma,\ \beta \neq \delta. \tag{3.21}$$

In the limit of weak selection, i.e. when $w \to 0$, as in the IP, from (3.19), (3.20) and (3.21) it follows that on a large star, under all dynamics As are favoured if and only if $a+b > c+d$, which is in agreement with the results of Tarnita *et al.* (2009) where the IP and the DB-B process in this case are considered.

It is shown (see Appendix B.2.5) that in the BD-D and DB-B processes,

$$\rho^{\mathrm{S}}_{\text{BD-D}} \gtreqless 1 \Leftrightarrow \alpha\beta \gtreqless \gamma\delta,\ \forall\, n, \tag{3.22}$$

$$\rho^{\mathrm{S}}_{\text{DB-B}} \gtreqless 1 \Leftrightarrow \alpha\beta \gtreqless \gamma\delta,\ \forall\, n. \tag{3.23}$$

In the case of weak selection, it follows from (3.22) and (3.23) that under the BD-D and the DB-B processes, As are favoured if and only if $a+b > c+d$, $\forall\, n$; this agrees with Tarnita *et al*. (2009) where the DB-B process is considered. In these dynamics, for $\alpha\beta = \gamma\delta$, $p^{AA}_{i,i+1} = p^{BB}_{n-i,n-i-1}$, $p^{AB}_{i,i} = p^{BA}_{n-i,n-i}$, $p^{BB}_{i,i-1} = p^{AA}_{n-i,n-i+1}$ and $p^{BA}_{i,i} = p^{AB}_{n-i,n-i}$. Hence, ${}^{A}P^{A}_{i} = {}^{B}P^{B}_{n-i}$, ${}^{A}P^{B}_{i} = {}^{B}P^{A}_{n-i}$, $T^{A}_{i} = T^{B}_{n-i}$, $T^{B}_{i} = T^{A}_{n-i}$ and therefore ${}^{A}T = {}^{B}T$, and ${}^{A}F^{A}_{i} = {}^{B}F^{B}_{n-i}$, ${}^{A}F^{B}_{i} = {}^{B}F^{A}_{n-i}$ and therefore ${}^{A}F = {}^{B}F$, $\forall\, 0 \le i \le n$.

Note that for the two birth-death processes (the IP and the BD-D process) there is a step change in $\rho^{\text{S}}_{\text{UR}}$ going from 0 to infinity in the limiting case of large n, so that for a small change in parameter values there is a huge change in the relative probabilities of fixation of the two strategies, whereas the change is gradual for the death-birth processes (VM and DB-B process).

On a complete graph, the condition for each of the strategies to be favoured in the VM is equivalent to that in the IP (see formula (2.121)). Similarly, we find that $\rho^{\text{CG}}_{\text{UR}}$ in the BD-D and DB-B processes also satisfies (2.121) in the case of a large population. Hence, As are favoured over Bs if $\alpha\left(\frac{\alpha}{\beta}\right)^{\left(\frac{\beta}{\alpha-\beta}\right)} > \delta\left(\frac{\delta}{\gamma}\right)^{\left(\frac{\gamma}{\delta-\gamma}\right)}$ and the step change described above occurs, in all processes. Thus, in the two processes where births occur first, evolution on a large star has similar characteristics to that on the complete graph of the same size, with the interaction of the whole population occurring through the central individual, which is continuously replaced. Note that for $\beta = \gamma$, $\rho^{\text{S}}_{\text{IP}} = \rho^{\text{CG}}_{\text{IP}}$ and for $\alpha = \delta$, $\rho^{\text{S}}_{\text{BD-D}} = \rho^{\text{CG}}_{\text{IP}}$. In the other two processes there is a big difference between the star and the complete graph, as a change in the central individual has a big impact on subsequent evolution on a star.

3.4 Numerical examples

3.4.1 The constant fitness case

In this case we assume that A individuals have constant relative fitness equal to r and B individuals fitness equal to 1.

The average fixation probability of a single mutant

In all dynamics ${}^{A}P \gtreqless 1/(n+1)$ if and only if $r \gtreqless 1$, and thus selection favours (opposes) the fixation of As when $r > 1$ $(r < 1)$. The relationship between fixation probabilities under the different dynamics we consider is shown in Table 3.1. Note that for $n > 3$, there is one and only one value of $r > 1$, $r_1(n)$, and one and only one value of $r < 1$, $r_2(n)$ (the exact values of $r_1(n)$ and $r_2(n)$ depend on n), such that ${}^{A}P_{\text{BD-D}} = {}^{A}P_{\text{VM}}$ (${}^{X}P_{\text{UR}}$ denotes the fixation probability of a single individual playing strategy X following the update rule UR). As n increases, $r_1(n)$ increases rapidly to infinity while $r_2(n)$ decreases rapidly to zero (the behaviour of $r_1(n)$ and $r_2(n)$ as the population size increases is shown in Figure 3.3). Thus, except for values of r more extreme than these critical values, as observed from Table 3.1, the birth-death processes yield a higher chance of fixation for a random mutant with $r > 1$ and less for a mutant with $r < 1$. The average fixation probability in some specific cases is shown in Figure 3.2.

When n is large we find that (see Appendices B.3.1 and B.3.2)

$$ {}^{A}P_{\text{IP}} \approx \frac{1-1/r^2}{1-1/r^{2n}},\ r \neq 1, \tag{3.24} $$

$$ {}^{A}P_{\text{BD-D}} \approx \frac{1-1/r}{1-1/r^{n}} = {}^{A}\mathrm{P}_{\mathrm{M}},\ r \neq 1, \tag{3.25} $$

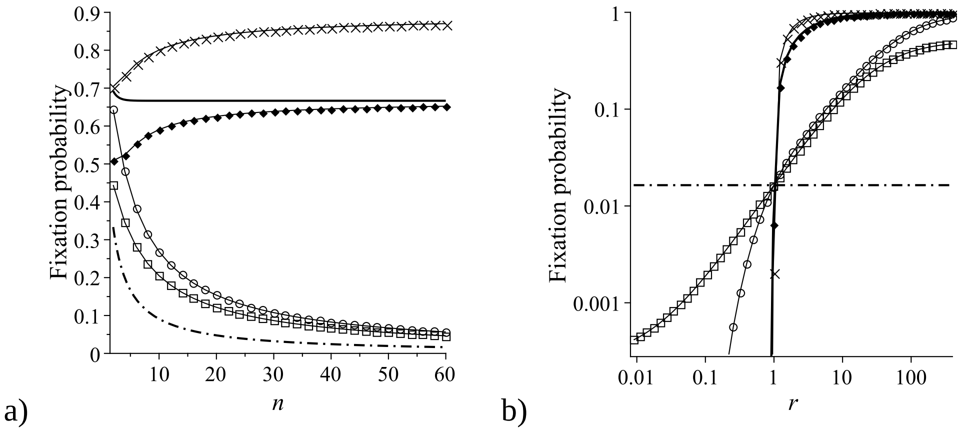
where ${}^{A}\mathrm{P}_{\mathrm{M}}$ is the fixation probability of a single mutant in the Moran process and on every circulation graph (see Section 1.5). Substituting (2.7)–(2.8) into (2.23) and using (3.5)–(3.12) appropriately, we get (see Appendix B.3.3) that in the case of constant fitness,

$$ {}^{A}P_{\text{VM}} = \frac{rn(r+1)}{(rn+1)(n+r)} \frac{r^2-1}{r^2 - \left(\frac{rn+1}{r(n+r)}\right)^{n-1}} < \frac{r+1}{n+1}, \tag{3.26} $$

$$ {}^{A}P_{\text{DB-B}} = \frac{1}{n+1}\left(\frac{1}{n+1} + \frac{r}{n+2r-1}\right)\frac{rn+1}{r+1} < \frac{r+1}{n-1} \tag{3.27} $$

and thus, in contrast to the birth-death processes, for the death-birth processes the increase of the population size decreases the chance of fixation to zero. For $r < 1$ the fixation probability of a mutant decreases with n in all dynamics.

As r decreases, the fixation probability under all dynamics decreases. Moreover, decreasing r to 0, the fixation probabilities under all dynamics but DB-B approach 0; ${}^{A}P_{\text{DB-B}}$ converges to $1/(n+1)^2$. Thus, following the DB-B process, even an invader mutant with almost zero fitness has a non-negligible chance to fixate, especially for small n. As r increases to infinity, ${}^{A}P_{\text{IP}}$ and ${}^{A}P_{\text{VM}}$ tend to 1, while ${}^{A}P_{\text{BD-D}}$ converges to $(1/(n+1))\,(1/(n+1)+n)$ and ${}^{A}P_{\text{DB-B}}$ to $(n/(n+1))(1/(n+1)+1/2)$. Hence, under the BD-D and DB-B processes, even for an infinite fitness r, the fixation of a mutant in a finite structured population can be significantly less than 1. This case appears even in a homogeneous well-mixed population of finite size under the DB-B process where the fixation probability of a single mutant tends to $1-1/(n+1)$ as r tends to infinity. This is due to the fact that fit individuals have a chance of not being chosen for reproduction, and individuals with low fitness have a chance to survive



a) b)

Figure 3.2: The average fixation probability of a single mutant on a star graph under the IP (crosses), the BD-D process (diamonds), the VM (circles) and the DB-B process (boxes), in the constant fitness case where (a) $r = 3$ and n varies, (b) $n = 60$ and r varies. The solid line represents the fixation probability in the Moran process and the dashed-dotted line represents the fixation probability of a single mutant in the case of neutral drift, $1/(n+1)$.

and reproduce, and eventually through evolution to spread and eliminate the individuals with higher fitness. Although in infinitely large homogeneous populations these replacements have negligible impact on the outcome of evolution, they might be important in finite populations, especially if these have a non-homogeneous structure under some evolutionary dynamics.

Mean time to absorption starting from a single mutant

Although the fixation of an advantageous mutant randomly placed on the star is more likely in the birth-death processes (except some special cases), absorption in these processes is reached slower than in the death-birth processes (except some extreme cases of $n > 4$ and $r \approx 0$). The comparison of the absorption times between the different dynamics is shown in Table 3.1. Figure 3.4 represents the absorption times for some specific values of r and n.

Here, we show explicit approximations of the absorption times starting from a single mutant given by (2.39) for extreme values of r.

For $r \approx 0$, in the IP and the VM, $\pi^{AB}_{i,i} \approx \pi^{BB}_{i,i-1} \approx 1$ and $\pi^{AA}_{i,i+1} \approx \pi^{BA}_{i,i} \approx 0$. In the BD-D process, for $i \neq 0$, $\pi^{AB}_{i,i} \approx 1$ and $\pi^{AA}_{i,i+1} \approx 0$. In the DB-B process, for $i \neq n$, $\pi^{BB}_{i,i-1} \approx 1$ and $\pi^{BA}_{i,i} \approx 0$. Given these approximations, following the same procedure as that shown in Section 2.3, we find that for $r \approx 0$

$$ {}^{A}T_{\text{IP}} \approx n(n-1)+1 > {}^{A}T_{\text{DB-B}}, \tag{3.28}$$

$$ {}^{A}T_{\text{BD-D}} \approx \frac{n^2+1}{n-1} + \frac{1}{n+1} > {}^{A}T_{\text{VM}}, \tag{3.29}$$

$$ {}^{A}T_{\text{VM}} \approx 1, \tag{3.30}$$

$$ {}^{A}T_{\text{DB-B}} \approx \frac{n}{n+1}\sum_{i=1}^{n-1}\left(\frac{1}{i}\right) + \frac{1}{n+1} + n > {}^{A}T_{\text{BD-D}} \ \ (\text{for } n > 4) \tag{3.31}$$

(${}^{X}T_{\text{UR}}$ denotes the mean time to absorption starting from a single individual playing strategy X following the update rule UR).

For $r \gg 1$, in the IP and the VM, $\pi^{AB}_{i,i} \approx \pi^{BB}_{i,i-1} \approx 0$ and $\pi^{AA}_{i,i+1} \approx \pi^{BA}_{i,i} \approx 1$. In the BD-D process, for $i \neq n$, $\pi^{BB}_{i,i-1} \approx 0$ and $\pi^{BA}_{i,i} \approx 1$. Finally, in the DB-B process, for $i \neq 0$, $\pi^{AB}_{i,i} \approx 0$ and $\pi^{AA}_{i,i+1} \approx 1$. Using these approximations and the formula (2.39), we find that for large $r \gg n$

$$ {}^{A}T_{\text{IP}} \approx \sum_{i=0}^{n-1}\frac{n(i+1)}{n-i} > {}^{A}T_{\text{VM}}, \tag{3.32}$$

$$ {}^{A}T_{\text{BD-D}} \approx n\left(n+\frac{1}{n+1}\right)\sum_{i=1}^{n-1}\left(\frac{1}{i}\right) + n + \frac{1}{n+1} > {}^{A}T_{\text{IP}}, \tag{3.33}$$

$$ {}^{A}T_{\text{VM}} \approx n^2 > {}^{A}T_{\text{DB-B}}, \tag{3.34}$$

$$ {}^{A}T_{\text{DB-B}} \approx \frac{n(n+3)}{2(n+1)}\sum_{i=1}^{n-1}\left(\frac{1}{i}\right) + \frac{n(n+1)+2}{2(n+1)}. \tag{3.35}$$

Note that in the DB-B process once there is an A individual on a leaf and in the centre, then the mean absorption time does not depend on r; specifically, substituting (3.9)–(3.12) and (2.7)–(2.8) appropriately into the formula giving T_1^A, (2.31), after some calculations it is proved that $T_1^A{}_{\text{DB-B}} = (n+1)\sum_{i=1}^{n-1} 1/i$.

Using the formulae of Section 2, we find that in the limit of a large population size, in the birth-death processes absorption occurs in a number of time steps that is $O(n^2 \ln n)$. However, in the death-birth processes, absorption is reached much faster, in $O(n)$ time steps.

In a large population, Figure 3.4 suggests that following the birth-death processes, absorption is reached slower for a value of r close to 1 (this value tends to 1 as the population size increases). Thus, in large populations neutral mutants yield higher absorption times. However, following the death-birth processes absorption time increases with the increase in r.

Table 3.1: Comparison of the average fixation probability and the mean times to absorption and fixation of a single mutant on a star graph in the constant fitness case between the IP, the BD-D process, the VM and the DB-B process. The variation of $r_1(n)$, $r_2(n)$, $r_3(n)$, $r_4(n)$, $r_5(n)$ and $r_6(n)$ with n is shown in Figure 3.3. Apart from some extreme cases, the two birth-death processes (IP and BD-D) yield a higher fixation probability for advantageous mutants ($r > 1$) and a lower fixation probability for disadvantageous mutants ($r < 1$) compared to the death-birth processes (VM and DB-B). On the other hand, death-birth processes yield much lower absorption and fixation times than birth-death processes

Comparison of fixation probabilities		
$n = 1$	$r \gtreqless 1$	${}^{A}P_{\text{IP}} = {}^{A}P_{\text{VM}} = {}^{A}\mathrm{P}_{\mathrm{M}} = r/(r+1)$ $r/(r+1) \gtreqless {}^{A}P_{\text{BD-D}} = {}^{A}P_{\text{DB-B}} = 1/2$
$n = 2,3$	$r > 1$	${}^{A}P_{\text{IP}} > {}^{A}\mathrm{P}_{\mathrm{M}} > {}^{A}P_{\text{VM}} > {}^{A}P_{\text{BD-D}} > {}^{A}P_{\text{DB-B}} > 1/(n+1)$
	$r < 1$	${}^{A}P_{\text{IP}} < {}^{A}\mathrm{P}_{\mathrm{M}} < {}^{A}P_{\text{VM}} < {}^{A}P_{\text{BD-D}} < {}^{A}P_{\text{DB-B}} < 1/(n+1)$
$n \geq 4$	$1 < r < r_1(n)$	${}^{A}P_{\text{IP}} > {}^{A}\mathrm{P}_{\mathrm{M}} > {}^{A}P_{\text{BD-D}} > {}^{A}P_{\text{VM}} > {}^{A}P_{\text{DB-B}} > 1/(n+1)$
	$1 < r_1(n) < r$	${}^{A}P_{\text{IP}} > {}^{A}\mathrm{P}_{\mathrm{M}} > {}^{A}P_{\text{VM}} > {}^{A}P_{\text{BD-D}} > {}^{A}P_{\text{DB-B}} > 1/(n+1)$
	$r < r_2(n) < 1$	${}^{A}P_{\text{IP}} < {}^{A}\mathrm{P}_{\mathrm{M}} < {}^{A}P_{\text{VM}} < {}^{A}P_{\text{BD-D}} < {}^{A}P_{\text{DB-B}} < 1/(n+1)$
	$r_2(n) < r < 1$	${}^{A}P_{\text{IP}} < {}^{A}\mathrm{P}_{\mathrm{M}} < {}^{A}P_{\text{BD-D}} < {}^{A}P_{\text{VM}} < {}^{A}P_{\text{DB-B}} < 1/(n+1)$
$\forall\, n$	$r = 1$	${}^{A}P_{\text{IP}} = {}^{A}\mathrm{P}_{\mathrm{M}} = {}^{A}P_{\text{BD-D}} = {}^{A}P_{\text{VM}} = {}^{A}P_{\text{DB-B}} = 1/(n+1)$

Comparison of absorption times		
$n = 1$	$\forall\, r$	${}^{A}T_{\text{IP}} = {}^{A}T_{\text{BD-D}} = {}^{A}T_{\text{VM}} = {}^{A}T_{\text{DB-B}} = 1$
$n = 2$	$1 < r < r_3(n)$	${}^{A}T_{\text{IP}} > {}^{A}T_{\text{BD-D}} > {}^{A}T_{\text{VM}} > {}^{A}T_{\text{DB-B}}$
	$1 < r_3(n) < r$	${}^{A}T_{\text{BD-D}} > {}^{A}T_{\text{IP}} > {}^{A}T_{\text{VM}} > {}^{A}T_{\text{DB-B}}$
	$r < 1$	${}^{A}T_{\text{BD-D}} > {}^{A}T_{\text{IP}} > {}^{A}T_{\text{DB-B}} > {}^{A}T_{\text{VM}}$
$n \geq 3$	$1 < r < r_3(n)$	${}^{A}T_{\text{IP}} > {}^{A}T_{\text{BD-D}} > {}^{A}T_{\text{VM}} > {}^{A}T_{\text{DB-B}}$
	$1 < r_3(n) < r$	${}^{A}T_{\text{BD-D}} > {}^{A}T_{\text{IP}} > {}^{A}T_{\text{VM}} > {}^{A}T_{\text{DB-B}}$
	$r < r_4(n) < 1\,^{*}$	${}^{A}T_{\text{IP}} > {}^{A}T_{\text{BD-D}} > {}^{A}T_{\text{DB-B}} > {}^{A}T_{\text{VM}}$
	$r_4(n) < r < 1$	${}^{A}T_{\text{BD-D}} > {}^{A}T_{\text{IP}} > {}^{A}T_{\text{DB-B}} > {}^{A}T_{\text{VM}}$
$\forall\, n$	$r = 1$	${}^{A}T_{\text{IP}} = {}^{A}T_{\text{BD-D}} > {}^{A}T_{\text{VM}} = {}^{A}T_{\text{DB-B}}$

Comparison of fixation times		
$n = 1$	$\forall\, r$	${}^{A}F_{\text{IP}} = {}^{A}F_{\text{BD-D}} = {}^{A}F_{\text{VM}} = {}^{A}F_{\text{DB-B}} = 1$
$n = 2$	$1 < r < r_5(n)$	${}^{A}F_{\text{IP}} > {}^{A}F_{\text{BD-D}} > {}^{A}F_{\text{DB-B}} > {}^{A}F_{\text{VM}}$
	$1 < r_5(n) < r$	${}^{A}F_{\text{BD-D}} > {}^{A}F_{\text{IP}} > {}^{A}F_{\text{DB-B}} > {}^{A}F_{\text{VM}}$
	$r < 1\,^{**}$	${}^{A}F_{\text{BD-D}} > {}^{A}F_{\text{IP}} > {}^{A}F_{\text{VM}} > {}^{A}F_{\text{DB-B}}$
$n \geq 3$	$1 < r < r_5(n)$	${}^{A}F_{\text{IP}} > {}^{A}F_{\text{BD-D}}$
	$1 < r_5(n) < r$	${}^{A}F_{\text{BD-D}} > {}^{A}F_{\text{IP}}$
	$1 < r < r_6(n)$	${}^{A}F_{\text{DB-B}} > {}^{A}F_{\text{VM}}$
	$1 < r_6(n) < r$	${}^{A}F_{\text{VM}} > {}^{A}F_{\text{DB-B}}$
	$r < 1\,^{**}$	${}^{A}F_{\text{BD-D}} > {}^{A}F_{\text{IP}} > {}^{A}F_{\text{VM}} > {}^{A}F_{\text{DB-B}}$
$\forall\, n$	$r = 1$	${}^{A}F_{\text{IP}} = {}^{A}F_{\text{BD-D}} > {}^{A}F_{\text{VM}} = {}^{A}F_{\text{DB-B}}$

[*] For $n > 4$ and $r \approx 0$, ${}^{A}T_{\text{IP}} > {}^{A}T_{\text{DB-B}} > {}^{A}T_{\text{BD-D}} > {}^{A}T_{\text{VM}}$.

[**] For $r \approx 0$, ${}^{A}F_{\text{BD-D}} > {}^{A}F_{\text{VM}} > {}^{A}F_{\text{IP}} > {}^{A}F_{\text{DB-B}}$.

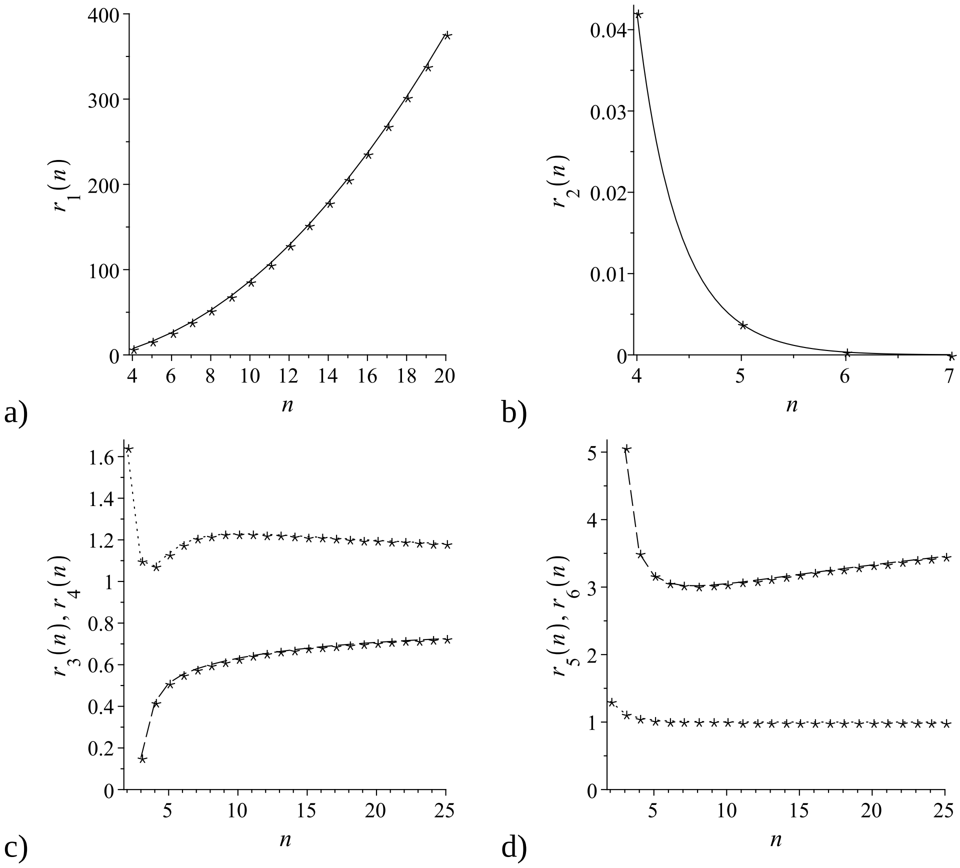


Figure 3.3: The behaviour of (a) $r_1(n)$, (b) $r_2(n)$, (c) $r_3(n)$ (dotted line) and $r_4(n)$ (dashed line), and (d) $r_5(n)$ (dotted line) and $r_6(n)$ (dashed line), as n increases (see Table 3.1).

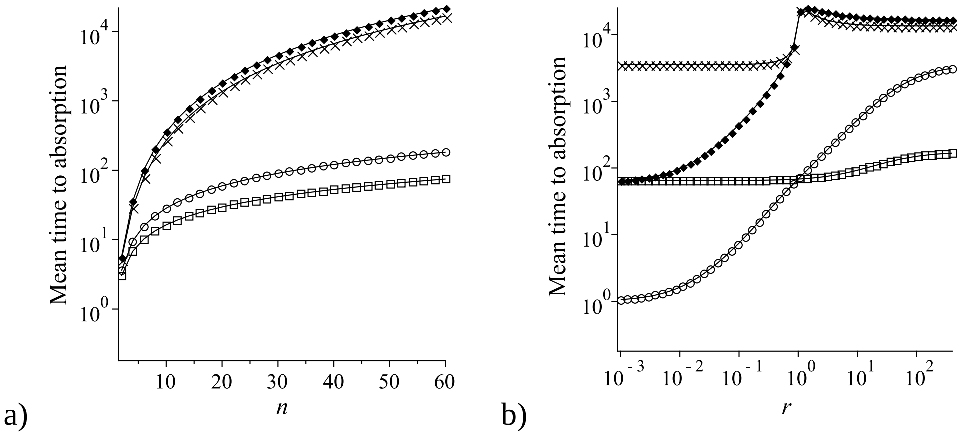


Figure 3.4: The mean time to absorption starting from a single mutant on a star graph under the IP (crosses), the BD-D process (diamonds), the VM (circles) and the DB-B process (boxes), in the constant fitness case where (a) $r = 3$ and n varies, (b) $n = 60$ and r varies.

Mean fixation time of a single mutant

As in the case of the absorption time, apart from some special cases of $r \approx 0$ where ${}^{A}F_{\text{VM}}$, for example, increases rapidly, the fixation time is generally higher in the

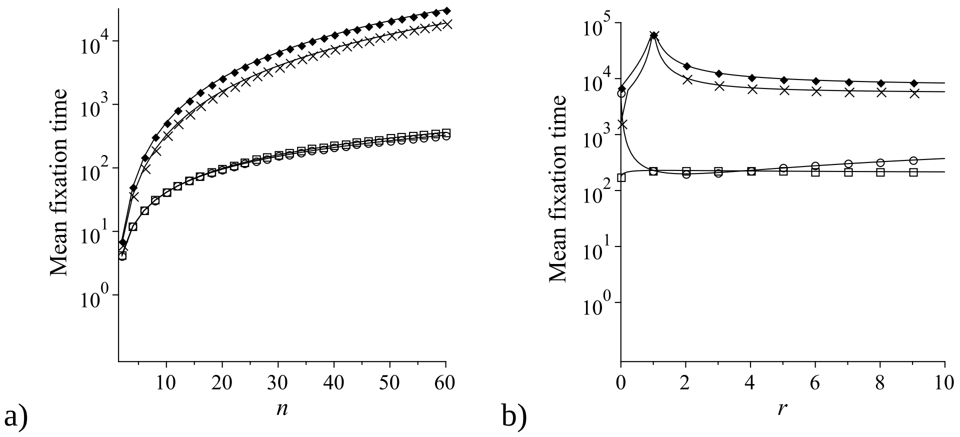


Figure 3.5: The mean fixation time of a single mutant on a star graph under the IP (crosses), the BD-D process (diamonds), the VM (circles) and the DB-B process (boxes), in the constant fitness case where (a) $r = 3$ and n varies, (b) $n = 40$ and r varies.

birth-death processes than the death-birth processes (${}^{X}F_{\text{UR}}$ denotes the mean fixation time of a single individual playing strategy X following the update rule UR). The comparison of the fixation times for various scenarios is shown in Table 3.1. Figure 3.5 shows an example of the mean fixation times of a single mutant as the population size and the mutant's fitness vary.

In the limit of a large r ($r \to \infty$), the fixation time of a single mutant in the IP and VM, ${}^{A}F_{\text{IP}}$ and ${}^{A}F_{\text{VM}}$, are equal to ${}^{A}T_{\text{IP}}$ given by (3.32) and ${}^{A}T_{\text{VM}}$ given by (3.34), respectively. In the BD-D and DB-B processes we find that

$$ {}^{A}F_{\text{BD-D}} \approx n(n+1)\sum_{i=1}^{n-1}\left(\frac{1}{i}\right) + n + \frac{1}{n+1}, \tag{3.36} $$

$$ {}^{A}F_{\text{DB-B}} \approx (n+1)\sum_{i=1}^{n-1}\left(\frac{1}{i}\right) + \frac{n(n+1)+2}{2(n+1)}. \tag{3.37} $$

The fixation times in the limiting case of $r \to 0$ are of less interest since in this case the chance of fixation of the mutant individual is very small and we condition on its fixation.

It should be noted that, especially in large populations, ${}^{A}F_{\text{DB-B}}$ is affected less by the change in r than the fixation times under other dynamics (as seen for ${}^{A}P_{\text{DB-B}}$ and ${}^{A}T_{\text{DB-B}}$ above).

In the limit of large population size, the fixation time in the birth-death processes is $O(n^3)$ while in the death-birth processes the limit is $O(n \ln n)$. Numerical examples suggest that in large populations, following the birth-death processes, as the absorption time, the mean fixation time of a neutral mutant is the highest.

3.4.2 The frequency dependent fitness case – example games on star graphs

In this section, we apply the results obtained in the previous sections to cases where the fitness of each individual depends on the composition of the population (frequency dependent fitness). We consider various evolutionary games which in an infinite well-mixed population result in different evolutionary outcomes.

A Hawk–Dove game on the star graph

The average fixation probability of a single mutant Hawk

Consider a Hawk–Dove game (see Section 1.3.1) described by the payoff matrix (1.19) played on a star graph.

The illustration of the dependence of the average fixation probability of a single Hawk on the star, ${}^{H}P$, on the population size and the fight cost, C, is shown in Figure 3.6 in an example. For comparison, in Figure 3.6b the respective fixation probabilities of a single Hawk when invading in a complete graph is also presented. As we have seen in Section 3.2.1, on the complete graph the update rules do not much influence the fixation probabilities, especially in relatively large populations. As in the constant fitness case, there is a step change in the fixation probability in all dynamics. If $\rho_{\text{UR}}^{\text{CG}} > 1$, mutants fixate with a probability almost independent of C; for $\rho_{\text{UR}}^{\text{CG}} < 1$, the fixation probability presents a rapid change and mutants' elimination becomes almost certain. However, different update rules yield considerably different results on a star graph.

Here, we can observe two qualitatively different behaviours, one for birth-death processes and another for death-birth processes. In the birth-death processes, for large n, ${}^{H}P$ exhibits a step function behaviour based on $\rho_{\text{UR}}^{\text{S}}$; in fact, for large n we find that (see Appendices B.3.1 and B.3.2)

$$ {}^{H}P_{\text{IP}} \approx \begin{cases} \frac{1-\frac{\gamma\delta}{\beta^2}}{1-\left(\frac{\gamma\delta}{\beta^2}\right)^n} \approx 1-\frac{\gamma\delta}{\beta^2}, & \rho_{\text{IP}}^{\text{S}} > 1 \\ 0, & \rho_{\text{IP}}^{\text{S}} < 1 \end{cases}, \tag{3.38} $$

$$ {}^{H}P_{\text{BD-D}} \approx \begin{cases} \frac{1-\frac{\delta}{\beta}}{1-\left(\frac{\delta}{\beta}\right)^n} \approx 1-\frac{\delta}{\beta}, & \rho_{\text{BD-D}}^{\text{S}} > 1 \\ 0, & \rho_{\text{BD-D}}^{\text{S}} < 1 \end{cases}. \tag{3.39} $$

On the other hand, in the death-birth processes, both ${}^{H}P_{\text{VM}}$ and ${}^{H}P_{\text{DB-B}}$ are bounded

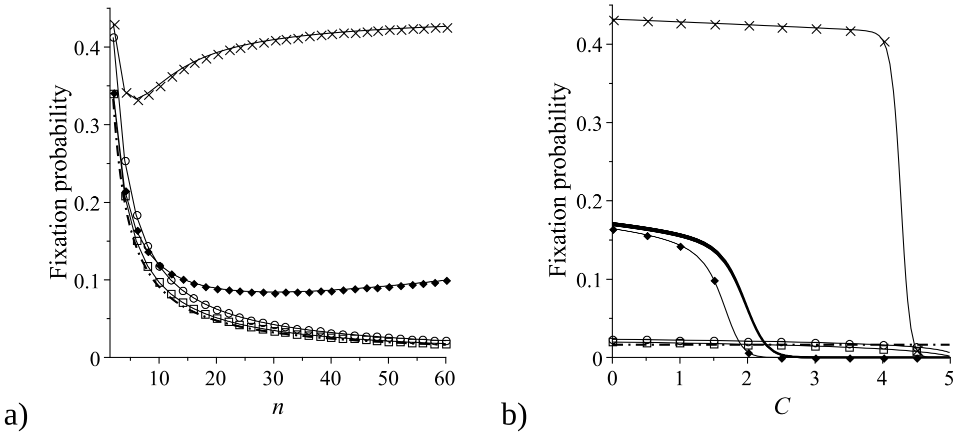


Figure 3.6: The average fixation probability of a single mutant Hawk on a star graph under the IP (crosses), the BD-D process (diamonds), the VM (circles) and the DB-B process (boxes), in the Hawk–Dove game described by the payoff matrix (1.19) in the case where (a) $V = 1$, $C = 1.5$ and n varies, (b) $n = 60$, $V = 1$ and C varies. $f_b = 2$ and $w = 1$. The thick lines represent the respective case on the complete graph and the dashed-dotted line represents the fixation probability of a single mutant in the case of neutral drift, $1/(n+1)$.

above by $(\beta + \delta)/\delta(n+1)$ (see Appendix B.3.3) and thus decrease to 0 as n increases to infinity.

Figure 3.6b suggests that when Hawks are favoured over Doves in the different update rules, the complete graph promotes the fixation of Hawks compared to the star graph in the BD-D, VM and DB-B process. Moreover, in the IP, favoured Hawks have much higher chance to fixate on a star graph.

Note that in the case of weak selection, in large stars and complete graphs, Hawks are favoured over Doves if the simple condition $C < 2V$ holds, in all update rules.

In the case where a mutant Dove invades into Hawks, all the above results can be easily obtained by interchanging the two strategies, i.e. by exchanging α and δ, and β and γ.

Mean time to absorption and fixation starting from a single mutant Hawk

A comparison of the absorption times for varying population size and varying fight cost, C, for the game with payoff matrix (1.19) is shown in Figure 3.7. The absorption times on the complete graph as C varies are also presented in Figure 3.7b for comparison. As shown in Section 3.2.1, the time needed for mutants to either fixate or die out on a complete graph is almost unaffected by the update rule followed. In large populations, values of the payoffs such that $\rho_{\mathrm{UR}}^{\mathrm{CG}} \approx 1$ lead to the highest times before absorption and fixation occur, in all the update rules. In con-

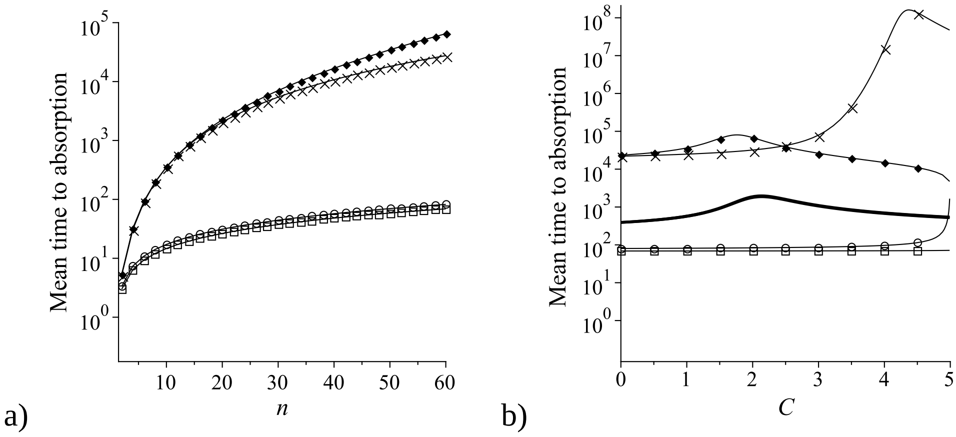


Figure 3.7: The mean time to absorption starting from a single mutant Hawk on a star graph under the IP (crosses), the BD-D process (diamonds), the VM (circles) and the DB-B process (boxes), in the Hawk–Dove game described by the payoff matrix (1.19) in the case where (a) $V = 1, C = 1.5$ and n varies, (b) $n = 60$, $V = 1$ and C varies. $f_b = 2$ and $w = 1$. The thick lines represent the respective case on the complete graph.

trast to the case of the complete graph, on the star graph, as in the constant fitness case, we observe that the speed to absorption and fixation might significantly vary when following different update rules. There is again a quantitative and qualitative distinction between birth-death and death-birth processes. In most of the cases the birth-death processes yield much higher absorption and fixation times than the death-birth processes. In large populations, both the absorption and fixation times in the two birth-death processes achieve local maxima for parameter values such that $\rho^{\text{S}}_{\text{IP}} \approx 1$ and $\rho^{\text{S}}_{\text{BD-D}} \approx 1$, since then the two strategies coexist for a long time before absorption/fixation occurs. In the VM and DB-B process, although the absorption and fixation times increase as C increases, they are affected less by the variation of C. In our example, we can see that for the VM as $C \to 5$ (i.e. the fitness of a Hawk individual when playing with just another Hawk tends to 0), ${}^{H}T_{\text{VM}}$ (and similarly ${}^{H}F_{\text{VM}}$) sharply increases. An initial Hawk on a leaf can be eliminated by chance, but if it is not, eventually it will occupy the center. At that moment, a Hawk on the leaves has a very very small fitness, so it will be eliminated and replaced by an offspring of the individual in the center; this process will be repeated many times before absorption occurs.

Figure 3.7b suggests that the process on the star might reach one of the two absorbing states much slower than on the complete graph when following the birth-death update rules, but much faster when following the death-birth update rules.

Prisoner's Dilemma on the star graph

Consider a Prisoner's Dilemma game (see Section 1.3.2) described by the payoff matrix (1.22) played on a star graph.

A cooperator and a defector in the centre of the star, respectively, have fitness

$$f_{C_c} = f_b + w\left(\frac{iB}{n} - C\right), \tag{3.40}$$

$$f_{D_c} = f_b + w\frac{iB}{n}, \tag{3.41}$$

given i cooperators on the n leaves. A cooperator on a leaf has fitness $f_b + w(B-C)$ against a cooperator in the centre and fitness $f_b - wC$ against a defector in the centre. Similarly, a defector on a leaf has fitness equal to $f_b + wB$ against a cooperator in the centre and fitness equal to f_b against a defector in the centre. Thus, a cooperator always does worse than a defector no matter its position and the composition of the population. By (3.22) and (3.23), in the BD-D and DB-B processes, cooperation is never favoured over defection for any intensity of selection and any population size. By (2.126) and (3.20) this is true under the IP and the VM as well in large populations. Moreover, by (2.91)–(2.94) and (3.1)–(3.12), the number of cooperators from any state and in any population size increases (decreases) by one with probability less than (greater than) or equal to the respective probability in the case of neutral drift. Thus, the fixation probability of cooperators starting from any possible state will always be less than that of neutral mutants, $i/(n+1)$ (apart from the DB-B process which can be equal to $i/(n+1)$). Hence, the star graph is not a good graph for the evolution of cooperation.

Numerical examples suggest that a single cooperator almost always has the highest chance of fixation following the two death-birth processes, with that in the DB-B process the highest and that in the IP the smallest one (see Figure 3.8). Similarly, the birth-death processes favour the fixation of a single defector into a population of cooperators while in the death-birth processes the cooperators' population has a higher chance to resist the invasion of a defector, with the fixation probability of the defector close to $1/(n+1)$, especially for a sufficiently large population. As in the Hawk–Dove game, the absorption and fixation times in the birth-death processes have important quantitative and qualitative differences from those in the death-birth processes. The times to absorption and fixation in the birth-death processes are much higher, mainly due to the large number of defector-defector replacements before their fixation.

Comparisons with the complete graph (see Figure 3.8b) indicate that in the IP,

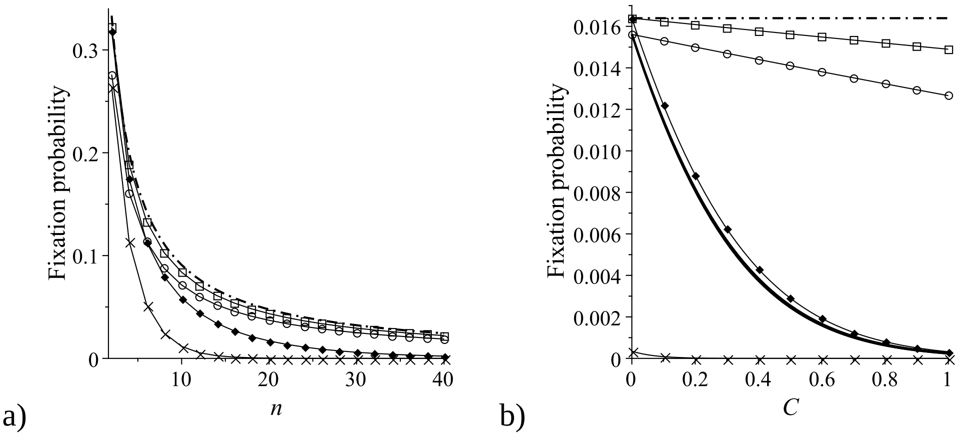


Figure 3.8: The average fixation probability of a single mutant cooperator on a star graph under the IP (crosses), the BD-D process (diamonds), the VM (circles) and the DB-B process (boxes), in the Prisoner's Dilemma game described by the payoff matrix (1.22) in the case where (a) $B = 2$, $C = 1$ and n varies, (b) $n = 60$, $B = 1$ and C varies. $f_b = 10$ and $w = 1$. The thick lines represent the respective case on the complete graph and the dashed-dotted line represents the fixation probability of a single mutant in the case of neutral drift, $1/(n+1)$.

the star graph impedes cooperation while in the BD-D, VM and DB-B processes it promotes cooperation (although as we have seen the probability of cooperators fixating is very small in all of these processes).

Coordination games on the star graph

Consider a Stag Hunt game (see Section 1.3.3) described by the payoff matrix (1.2) played on the star graph. Strategy A is Pareto efficient ($a > d$) and strategy B is risk dominant ($a+b < c+d$). On a large star graph, in the case of weak selection the risk dominant strategy is always favoured over the Pareto efficient strategy (since $c+d$ is higher than $a+b$), in all the update rules. For any non-zero intensity of selection, since $a+b < c+d$ and $a > c > d > b$, $\alpha\beta$ is lower than $\gamma\delta$ as well and thus the BD-D and DB-B processes always favour the risk dominant strategy over the Pareto efficient strategy on a star graph of any size. It is shown numerically that this holds for the IP and the VM as well. Numerical examples also indicate that in none of the update rules is the fixation of strategy A favoured by selection, i.e. ${}^{A}P$ is always less than $1/(n+1)$ in all update rules.

However, in a coordination game where B is not the risk dominant strategy, i.e. A is both the Pareto efficient and risk dominant strategy ($a > d$ and $a+b > c+d$), then A might be favoured over B for any non-zero intensity of selection in all the update rules. In addition, it is shown that selection might favour the fixation of A and oppose the fixation of B, i.e. ${}^{A}P > 1/(n+1) > {}^{B}P$, under any of the update rules. Moreover, the chance of As' fixation remains relatively small. Figure 3.9

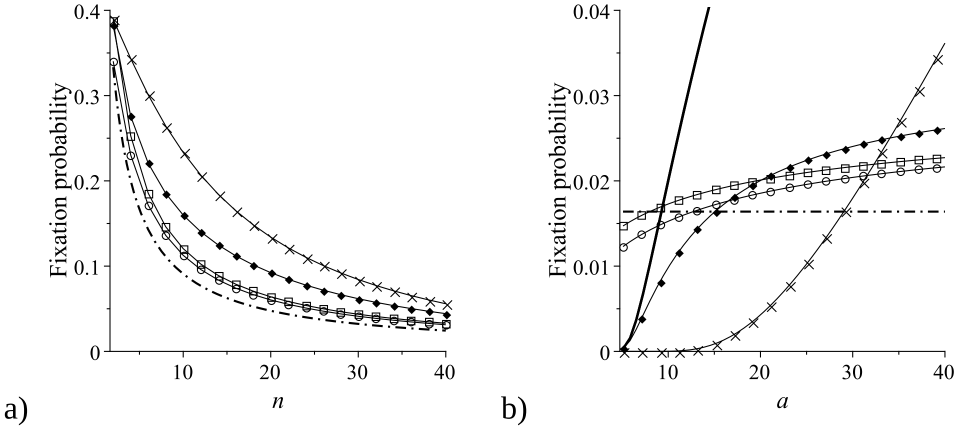


Figure 3.9: The average fixation probability of a single mutant playing strategy A on a star graph under the IP (crosses), the BD-D process (diamonds), the VM (circles) and the DB-B process (boxes), in a coordination game in the case where (a) $a = 35$ and n varies, (b) $n = 60$ and a varies. $b = 3$, $c = 5$, $d = 4$, $f_b = 2$ and $w = 1$. The thick lines represent the respective case on the complete graph and the dashed-dotted line represents the fixation probability of a single mutant in the case of neutral drift, $1/(n+1)$.

shows the average fixation probability of a single A on the star for an example set of parameters, as the population size and the payoff a, vary. The respective probability in the case of the complete graph is also presented in Figure 3.9b. We again observe that in large stars, in the two birth-death processes IP and BD-D, values of payoffs such that $\rho^{\mathrm{S}}_{\mathrm{IP}} < 1$ and $\rho^{\mathrm{S}}_{\mathrm{BD\text{-}D}} < 1$ result in an almost zero fixation probability while a rapid increase in the fixation probability occurs as $\rho^{\mathrm{S}}_{\mathrm{IP}}$ and $\rho^{\mathrm{S}}_{\mathrm{BD\text{-}D}}$ become bigger than 1. The most advantageous update rule for the fixation of strategy A can be either the IP, the BD-D process or the DB-B process. Numerical examples indicate that the fixation probability of strategy A under the VM is always lower than that in the DB-B process. In this game, the speed of the evolutionary process is again much slower in the birth-death processes with the fixation time of mutants in large populations highest when $\rho^{\mathrm{S}}_{\mathrm{IP}} \approx 1$ and $\rho^{\mathrm{S}}_{\mathrm{BD\text{-}D}} \approx 1$.

Comparisons of the results on the star with those on the complete graph suggest that apart from cases where the payoff a is much larger than the other payoffs and the population size is relatively small, in the two birth-death processes the heterogeneity of the star graph inhibits the spread of strategy A. However, in the two death-birth processes, the star might be a better graph for As to spread.

3.5 Discussion

In this chapter, we have investigated analytically stochastic evolutionary processes on the simplest irregular graph, the star graph. Using the formulae of the fixation probability and absorption and fixation times derived in Section 2.3, we have studied the process under different update rules, in various evolutionary games which result in different evolutionary outcomes in infinitely large homogeneous well-mixed populations. It has been shown that although the choice of the update rule of the evolutionary process does not significantly affect the evolution of mutants on homogeneous populations, it might cause considerable differences if these invade in a population with a non-homogeneous structure. However, in most of the cases, these differences are mainly due to the extreme structure of the graph rather than the dynamics themselves.

The IP in combination with the specialness of the star, enhances significantly the selection pressure and outweighs drift. At least for the cases where a mutant always does better (worse) than a resident individual, for example in the constant fitness case and the Prisoner's Dilemma, the fixation probability of mutants is always higher (lower) than the respective probability on a complete graph of the same size. This happens only in the IP. In the DB-B process the selection pressure is considerably nullified and random drift is emphasised partly due to the dynamics itself but mainly due to properties of the star graph. When an individual on a leaf dies randomly, which is the usual event, especially in large populations, it is inevitably replaced by the offspring of the individual in the centre (the fitness of individuals does not contribute to the process). If the individual in the centre dies (with probability $1/(n+1)$) then it is replaced by the offspring of an individual on the leaves which is chosen with probability proportional to fitness, and thus the fitness of the individual in the centre is irrelevant. Hence, especially in large populations, the spread and fixation of mutants happens almost randomly. In the BD-D process, although the first event happens randomly as well, since the increase or decrease of mutants on the leaves depends on the fitness of the individuals in this position, the contribution of the fitness in the BD-D process is much higher than that in the DB-B process. Finally, in the VM, although selection operates on $n+1$ individuals (as in the IP), the process on the star is a strong suppressor of fitness. In this process, especially in large populations, the individual in the centre is quite safe and occupying this position at the beginning of the process is highly advantageous. However, the most likely initial position is a leaf, a position from which the role of the fitness is diminished. Hence, in most of the cases, birth-death processes yield higher (lower) fixation probabilities of advantageous (disadvantageous) mutants than the death-birth processes. However, these processes usually require exceedingly long times to fixation, which are much larger than the respective times in the death-birth processes.

For the BD-D and DB-B processes, where the first event happens randomly, we have seen that even a mutant with infinite fitness has a chance of not fixating which is independent of its fitness. On the other hand, in the DB-B process, even an invader mutant with almost zero fitness has a small chance to fixate which does not depend on its fitness. Hence, both the update rule and the structure of the population might result in a relatively high chance of fixation of the less fit individuals and the elimination of the fitter individuals even in these extreme cases.

Most of the previous studies of evolutionary processes on graphs have considered the case of weak selection. It has been shown that in this case, following the rules of the IP and DB-B process, mutants on a large star playing strategy A are favoured over residents playing strategy B if $a+b>c+d$ (Tarnita *et al.*, 2009). We have shown that this condition holds for the BD-D process and the VM as well. In addition, for each of the dynamics we have found appropriate conditions for strategy A to be favoured over strategy B for any intensity of selection. Especially in the BD-D and DB-B processes, we have shown that mutant individuals playing strategy A on a star of any size are favoured over Bs if the simple condition $\alpha\beta>\gamma\delta$ holds. In the case where $\alpha\beta=\gamma\delta$, the fixation probability as well as the absorption and fixation time of a number of individuals of either type in a population of the other type are identical for any population size.

When a strategy A loses the advantage it has over strategy B and Bs become favoured, the average fixation probability of a mutant individual playing strategy A on a large star tends rapidly to zero when following the two birth-death processes. At this point, the fixation time takes the highest value. This also happens in the well-mixed population. Birth-death dynamics on a star effectively act like a well-mixed population when the population size is large, as the central vertex is continuously replaced and all the others have the same relationship to each other through it. For death-birth dynamics this does not happen since the dynamics are very different. The central vertex is highly important and occupying it is a great advantage. In both processes, the increase of the population size results in an important decrease of the contribution of the fitness in the evolutionary process and the probability of fixation is close to $1/(n+1)$, as occupying the centre or not at the start is the key event. In particular, in the DB-B process, a single random event can cause big changes in the evolutionary process on the star irrespective of the fitness of individuals.

Considering the evolution of cooperation in the Prisoner's Dilemma we have seen that the heterogeneity of the star is an inhospitable environment for cooperation to evolve. It is proved that cooperation is never favoured by selection while defection is always favoured, in all update rules. However, it has been shown that there are update rules under which cooperation is encouraged more on the star than on the complete graph. In a similar way, in a Stag Hunt type of game it is difficult for the Pareto efficient strategy to evolve on the star. In particular, it is shown that in all update rules the risk dominant strategy is always favoured over the Pareto efficient strategy, and selection never favours the Pareto efficient strategy.

The investigation of the evolutionary process on the star graph under four update rules has demonstrated that both the structure of the population and the update rule when applied in a non-homogeneous structure might have an important influence on the outcome of the evolutionary dynamics. However, it is not clear to what extent the reported characteristics depend upon the unique character of the star. So far, almost all the other analytical investigations have involved regular graphs where the differences of the evolutionary process under different update rules are relatively minor. On the other hand, it is likely that whilst other irregular graphs may display properties of the star, behaviour will in general not be as extreme as that observed on the star (see Broom *et al.*, 2009). Thus, it would be of interest to investigate whether, and to what extent, some of the observed phenomena hold for larger classes of graphs.

CHAPTER 4

Evolutionary dynamics on complex graphs

4.1 Introduction

In Chapters 2 and 3, we have seen that an analytic approach of the evolutionary dynamics is possible when individuals of the population occupy the vertices of simple graphs with a lot of symmetry and lack of complexity. Such graphs are the complete graph (Taylor *et al*., 2004), the circle (Ohtsuki and Nowak, 2006a; Broom *et al*., 2010a), the star (Broom and Rychtář, 2008; Broom *et al*., 2010a; Hadjichrysanthou *et al*., 2011) and the line (Broom and Rychtář, 2008). See also Lieberman *et al*. (2005). Moreover, real populations have some complex structures where the analytic investigation of the dynamics is usually impossible, especially when the fitness of individuals depends on the composition of the population, due to the large number of the possible configurations of the population through evolution. In such cases the use of approximation methods is essential. The investigation of evolutionary models on complex graphs is often limited to individual-based stochastic simulations that can be difficult to validate, time consuming to run and the results generated can lack generality. To tackle this problem, researchers from different areas have developed different techniques that allow us to derive low-dimensional ODE (ordinary differential equation) models that, under certain assumptions about the structure of the network and the dynamics running on it, can approximate well the average outcome from stochastic network simulations. Establishing the clear relation between the exact-stochastic and approximate model is challenging since this requires a mathematical handle on both solutions as well as the formulation of an appropriate limit in which the exact-stochastic model approaches the deterministic limit. One such well known class of approximate models is that of the *pairwise models* (e.g., Matsuda *et al.*, 1992; van Baalen and Rand, 1998; Keeling, 1999; Eames and Keeling, 2002; House and Keeling, 2011) where the dynamics at the vertex level, in a population with graph-like contact structure, is described in terms of the dynamics of pairs of individuals, and the hierarchical dependence on higher order structures is cut off via an appropriately constructed closure. In recent years, other models of similar nature have been derived, for example, the *Probability Generating Function* approach (Volz and Meyers, 2007; Volz, 2008) and more notably the *Effective Degree model* (Lindquist *et al.*, 2011). These models have arisen in the context of epidemiology but their formulation and properties makes them amenable to be used for the modelling of evolutionary game dynamics on graphs.

In this chapter, using the techniques of the Effective Degree model (Lindquist *et al.*, 2011) we consider evolutionary game dynamics when individuals interact on different complex graphs playing two strategies, A and B. The game played is described by the payoff matrix (1.2). Individuals update their strategies following the update rules of the biased voter model (VM) as described in Section 3.2 (see also Antal *et al.*, 2006). VM type dynamics is one of the classical interacting particle systems which has been applied to many evolutionary processes, from opinion and culture dynamics to processes in population genetics and kinetics of catalytic reactions (e.g., Liggett, 1985; Frachebourg and Krapivsky, 1996; San Miguel *et al.*, 2005; Castellano *et al.*, 2009), and has received considerable attention.

We show that for randomly or proportionately mixed networks, with or without degree heterogeneity, the model constructed, called the *Neighbourhood Configuration* model, provides an excellent approximation to output from simulation models, even for relatively small graph sizes. Following the same evolutionary dynamics we also construct a pairwise model and highlight its merits and shortcomings when compared to the Neighbourhood Configuration model. As an example, we consider the evolutionary process in a Hawk–Dove game when played in three types of graph which have been widely used; a random regular graph, a random graph and a scale-free network.

4.2 Approximate models of evolutionary game dynamics on graphs

4.2.1 Pairwise model

In this section, we first approach the evolutionary process by using the pair approximation method (Matsuda *et al.*, 1992; van Baalen and Rand, 1998; Keeling, 1999;

Eames and Keeling, 2002; House and Keeling, 2011). This is a method where the frequency of higher order moments, such as triples composed of three vertices connected in a line, is approximated by the frequency of lower order moments, such as pairs and single vertices. This method works well with graphs with no or little heterogeneity in the number of connections, but can be extended to more heterogeneous graphs with a significant increase in the number of equations. Such methods assume that the underlying graphs have undirected edges and that these are either unweighted or uniformly weighted. This approximation method has been used in previous work for the investigation of the evolutionary process in structured populations under different update rules (e.g., Morris, 1997; Hauert and Doebeli, 2004; Hauert and Szabó, 2005; Ohtsuki *et al.*, 2006; Ohtsuki and Nowak, 2006b; Morita, 2008; Fu *et al.*, 2010). Here, we follow a similar procedure to approach the process when the update rules of the VM are followed.

Assume a population of N individuals playing either strategy A or strategy B placed on a regular graph of degree k. Let p_A (p_B) denote the proportion of A (B) individuals in the population and p_{AB} the frequency of AB pairs. Let also $q_{B|A}$ denote the conditional probability that a neighbour of a chosen A individual is a B individual, i.e. $q_{B|A} = p_{AB}/(p_{AA} + p_{AB}) = p_{AB}/p_A$ (thus $1 - q_{B|A} = q_{A|A} = p_{AA}/p_A$ denotes the conditional probability that a neighbour of a chosen A individual is another A individual). The equivalent expressions also hold for $q_{A|B}$ and $q_{B|B}$. The edges of the graphs we consider are assumed to be undirected and therefore $p_{AB} = p_{BA}$.

Since all the vertices of the graph are assumed to be topologically equivalent, every pair of A (B) individuals is equally likely to be connected with probability $q_{A|A}$ $(q_{B|B})$. The probability that from the k connections of an A individual, i of them are with other As (and thus $k-i$ are with Bs), $l_A(i)$, is approximated by assuming that it follows a binomial distribution. This is given by

$$l_A(i) = \binom{k}{i} {q_{A|A}}^i \left(1 - q_{A|A}\right)^{k-i} = \frac{k!}{i!(k-i)!} {q_{A|A}}^i {q_{B|A}}^{k-i}. \tag{4.1}$$

Similarly, the probability that a B individual is connected with i As and $k-i$ Bs is assumed to be given by

$$l_B(i) = \binom{k}{i} \left(1 - q_{B|B}\right)^i {q_{B|B}}^{k-i} = \frac{k!}{i!(k-i)!} {q_{A|B}}^i {q_{B|B}}^{k-i}. \tag{4.2}$$

As defined in Section 2.4 , the fitness of each individual is assumed to be equal to $f = f_b + wP$, where P is the average payoff obtained by the games played with neighbouring individuals, f_b is a constant background fitness of individuals and $w \in [0,\infty)$ represents the intensity of selection which determines the contribution of P to fitness. An A individual which is connected with i other A individuals has fitness equal to

$$f_A(i) = f_b + w\left(\frac{ia+(k-i)b}{k}\right). \tag{4.3}$$

A B individual which is connected with i As has fitness equal to

$$f_B(i) = f_b + w\left(\frac{ic+(k-i)d}{k}\right). \tag{4.4}$$

Let us denote by $\overline{F}$ the sum of the inverse of the fitnesses of all individuals,

$$\overline{F} = p_A \sum_{i=0}^{k} \frac{l_A(i)}{f_A(i)} + p_B \sum_{i=0}^{k} \frac{l_B(i)}{f_B(i)}. \tag{4.5}$$

The probability that an A individual dies (with probability inversely proportional to its fitness) and is replaced by a randomly selected neighbouring B individual, $P_{A\to B}$, is given by

$$P_{A\to B} = \frac{p_A}{\overline{F}} \sum_{i=0}^{k} \frac{l_A(i)}{f_A(i)} \cdot \frac{k-i}{k}. \tag{4.6}$$

One of the B individuals dies with probability inversely proportional to its fitness and is replaced by a random neighbouring A individual with probability

$$P_{B\to A} = \frac{p_B}{\overline{F}} \sum_{i=0}^{k} \frac{l_B(i)}{f_B(i)} \cdot \frac{i}{k}. \tag{4.7}$$

The rate of increase of the frequency of A individuals, p_A, (given one transition in each iteration step) is given by the following equation

$$\begin{aligned} \dot{p}_A &= \frac{1}{N}P_{B\to A} - \frac{1}{N}P_{A\to B} \\ &= \frac{1}{N\overline{F}} \sum_{i=0}^{k} \frac{(k-1)!}{i!(k-i)!} \left(p_B {q_{A|B}}^{i} {q_{B|B}}^{k-i} \frac{i}{f_B(i)} - p_A {q_{A|A}}^{i} {q_{B|A}}^{k-i} \frac{k-i}{f_A(i)} \right). \end{aligned} \tag{4.8}$$

When an A individual connected to i other As is replaced by a B individual, the number of AA pairs decreases by i and therefore the frequency of AA pairs, p_{AA}, decreases by $i/(kN/2)$ ($kN/2$ is the total number of edges). This happens with probability

$$P_{AA\to AB} = \frac{p_A}{\overline{F}} \frac{l_A(i)}{f_A(i)} \cdot \frac{k-i}{k}. \tag{4.9}$$

Similarly, the number of AA pairs increases by i and therefore p_{AA} increases by $i/(kN/2)$ when a B connected to i As is replaced by an A. This happens with probability

$$P_{AB\to AA} = \frac{p_B}{\overline{F}} \frac{l_B(i)}{f_B(i)} \cdot \frac{i}{k}. \tag{4.10}$$

According to the above, the rate of increase of the frequency of AA pairs (given one transition in each iteration step) is given by the following equation

$$\begin{aligned}\dot{p}_{AA} &= \sum_{i=0}^{k} \frac{2i}{kN} P_{AB\to AA} - \sum_{i=0}^{k} \frac{2i}{kN} P_{AA\to AB} \\ &= \frac{2}{kN\overline{F}} \sum_{i=1}^{k} \frac{(k-1)!}{(i-1)!(k-i)!} \left(p_B {q_{A|B}}^{i} {q_{B|B}}^{k-i} \frac{i}{f_B(i)} - p_A {q_{A|A}}^{i} {q_{B|A}}^{k-i} \frac{k-i}{f_A(i)} \right).\end{aligned} \tag{4.11}$$

Since, $p_A + p_B = 1$, $p_{AB} = p_{BA} = p_A - p_{AA}$ and $p_{BB} = 1 - p_{AA} - 2p_{AB}$, the system can be described by just two dynamical equations, say (4.8) and (4.11). Note that the frequency of larger clusters can be approximated by the frequencies of the pairs. For example, the frequency of the three cluster XYZ, p_{XYZ}, can be approximated by $p_{XY}p_{YZ}/p_Y$.

4.2.2 Neighbourhood Configuration model

The effective degree model (Lindquist *et al.*, 2011) stems from a model first proposed by Ball and Neal (2008) in the context of an *SIR* type infectious disease transmission model, where vertices in a graph are accounted for not only by their disease status but also by their number of susceptible S and infected I neighbours, referred to as the effective degree of the vertices. Keeping track of recovered neighbours R is not important as they play no part in the dynamics. Lindquist *et al.* (2011) formalised this model by categorising each vertex according to its disease state as well as the number of its neighbours in the various disease states. Based on heuristic arguments and on the assumption of proportionate mixing, Lindquist *et al.* (2011) derived a system of ODEs in terms of susceptible and infected vertices with all possible neighbourhood configurations. In this chapter, we adopt this method to approach the stochastic evolutionary dynamics in a two-strategy game played on complex graphs.

Assume, as above, that a resident population of B individuals placed on an undirected and connected static graph is invaded by a number of mutant A individuals. The evolutionary dynamics of the evolutionary process is described by the update rules of the VM. Each individual on the graph is classified according to its strategy and the number of its connected individuals playing each of the strategies. Let us denote by $M_{m,r}$ ($R_{m,r}$) the number of individuals in the class where individuals play the mutant (resident) strategy and each of them is connected to m other mutant individuals and r residents. Consider m and r as the number of edges that start from an individual of an $M_{m,r}$ or $R_{m,r}$ class and end at a mutant or a resident, respectively. Assume that the maximum degree of a vertex on the graph is $D_{\max}$ and therefore $m \geq 0$, $r \geq 0$ and $1 \leq m+r \leq D_{\max}$. Hence, the number of different classes is equal to $\sum_{k=1}^{D_{\max}} 2(k+1) = D_{\max}(D_{\max}+3)$.

The sum of the inverse of the fitnesses of all individuals, $\overline{F}$, is given by

$$\overline{F} = \sum_{k=1}^{D_{\max}} \sum_{i+j=k} \left(M_{i,j} \frac{1}{(i\alpha + j\beta)/(i+j)} + R_{i,j} \frac{1}{(i\gamma + j\delta)/(i+j)} \right), \tag{4.12}$$

where $\alpha = f_b + wa$, $\beta = f_b + wb$, $\gamma = f_b + wc$ and $\delta = f_b + wd$. Let us also define some terms which will be useful in subsequent calculations. Let L_{XY} be the number of edges which connect an individual of type X to an individual of type Y (with X and Y being the start and destination vertex, respectively), where X and Y denotes either a mutant (M) or a resident (R) individual.

$$\begin{aligned} L_{\mathrm{MR}} &= \sum_{k=1}^{D_{\max}} \sum_{i+j=k} jM_{i,j}, \quad & L_{\mathrm{RM}} &= \sum_{k=1}^{D_{\max}} \sum_{i+j=k} iR_{i,j}, \\ L_{\mathrm{MM}} &= \sum_{k=1}^{D_{\max}} \sum_{i+j=k} iM_{i,j}, \quad & L_{\mathrm{RR}} &= \sum_{k=1}^{D_{\max}} \sum_{i+j=k} jR_{i,j}. \end{aligned} \tag{4.13}$$

In addition, we use the following notation:

$$\begin{aligned} H_1 &= \sum_{k=1}^{D_{\max}} \sum_{i+j=k} \frac{ij}{i\alpha + j\beta}(M_{i,j} - \delta_{mr}^{ij}), \quad & H_2 &= \sum_{k=1}^{D_{\max}} \sum_{i+j=k} \frac{ij}{i\gamma + j\delta}(R_{i,j} - \delta_{mr}^{ij}), \\ H_3 &= \sum_{k=1}^{D_{\max}} \sum_{i+j=k} \frac{i^2}{i\gamma + j\delta} R_{i,j}, \quad & H_4 &= \sum_{k=1}^{D_{\max}} \sum_{i+j=k} \frac{j^2}{i\alpha + j\beta} M_{i,j}, \end{aligned} \tag{4.14}$$

where δ_{mr}^{ij} is a function defined as

$$\delta_{mr}^{ij} = \begin{cases} 1, & i = m, j = r \\ 0, & \text{otherwise} \end{cases}. \tag{4.15}$$

An individual might move from one class to another, either by the change of its strategy or due to the change of a neighbour's strategy. The probability that an A mutant individual of the $M_{m,r}$ class is replaced by a B resident individual and move to the $R_{m,r}$ class is equal to the probability that this individual is selected for death (with probability inversely proportional to its fitness) and is replaced by the offspring of one of its neighbouring residents (which is chosen at random). This probability is equal to

$$\frac{\frac{1}{(m\alpha+r\beta)\big/(m+r)}}{\overline{F}}\cdot\frac{r}{m+r}=\frac{r}{\overline{F}(m\alpha+r\beta)}. \tag{4.16}$$

Similarly, an individual of the $R_{m,r}$ class moves to the $M_{m,r}$ class with probability

$$\frac{\frac{1}{(m\gamma+r\delta)\big/(m+r)}}{\overline{F}}\cdot\frac{m}{m+r}=\frac{m}{\overline{F}(m\gamma+r\delta)}. \tag{4.17}$$

A mutant connected to m other mutants and r residents leaves the $M_{m,r}$ class and enters the $M_{m+1,r-1}$ class when a neighbouring resident is replaced by a mutant. The probability of such a movement is approximated in the following way. The probability that a resident individual from an $R_{i,j}$ class is selected to die and is replaced by an offspring of a mutant neighbour is equal to

$$R_{i,j}\frac{\frac{1}{(i\gamma+j\delta)\big/(i+j)}}{\overline{F}}\cdot\frac{i}{i+j}=R_{i,j}\frac{i}{\overline{F}(i\gamma+j\delta)}. \tag{4.18}$$

We now use an approximation to estimate the probability that a resident individual which is replaced by a mutant is connected to a mutant from the $M_{m,r}$ class. This is assumed to be equal to the probability that a randomly chosen edge which connects a resident individual with a mutant (starts from a resident and ends at a mutant), is an edge which connects the replaced resident with that mutant individual from the $M_{m,r}$ class (i edges connect the replaced resident with a mutant and r edges connect an individual of the $M_{m,r}$ with a resident, and so there are ir different ways of having such a connection). This probability is given by

$$\frac{ir}{\sum\limits_{k=1}^{D_{\max}}\sum\limits_{i+j=k} iR_{i,j}}. \tag{4.19}$$

Hence, the probability that a mutant from the $M_{m,r}$ class moves to the $M_{m+1,r-1}$ class can be approximated by

$$\sum_{k=1}^{D_{\max}}\sum_{i+j=k}R_{i,j}\frac{\frac{1}{(i\gamma+j\delta)\big/(i+j)}}{\overline{F}}\cdot\frac{i}{i+j}\cdot\frac{ir}{\sum\limits_{k=1}^{D_{\max}}\sum\limits_{i+j=k} iR_{i,j}}=\frac{H_3 r}{\overline{F}L_{\mathrm{RM}}}. \tag{4.20}$$

In the same way, the probability that a mutant individual from the $M_{m,r}$ class moves to the $M_{m-1,r+1}$ class is equal to the probability that a neighbouring mutant of that individual is replaced by a resident. The probability of such a transition is approximated by the probability that a mutant individual of the population dies, is then replaced by a neighbouring resident individual, and the replaced individual is connected to the mutant from the $M_{m,r}$ class, i.e. by the probability

$$\sum_{k=1}^{D_{\max}} \sum_{i+j=k} (M_{i,j} - \delta_{mr}^{ij}) \frac{\frac{1}{(i\alpha+j\beta)/(i+j)}}{\overline{F}} \cdot \frac{j}{i+j} \cdot \frac{im}{\sum\limits_{k=1}^{D_{\max}} \sum\limits_{i+j=k} iM_{i,j} - m} = \frac{H_1 m}{\overline{F}(L_{\mathrm{MM}} - m)}. \tag{4.21}$$

The term $M_{i,j} - \delta_{mr}^{ij}$ represents the number of mutants in an $M_{i,j}$ class that can be replaced by a resident such that the transition of a mutant from the $M_{m,r}$ class to the $M_{m-1,r+1}$ class is possible. When $i = m$ and $j = r$, 1 is subtracted from $M_{m,r}$ because the movement of an individual from the $M_{m,r}$ to the $M_{m-1,r+1}$ cannot be a result of its own replacement. In other words, if a mutant from the $M_{m,r}$ class dies and is replaced by a resident, there are other $M_{m,r} - 1$ mutants from that class that might be connected to it and thus move to the $M_{m-1,r+1}$ class. The term $\sum_{k=1}^{D_{\max}} \sum_{i+j=k} iM_{i,j} - m$ corresponds to the number of edges that connect any mutant (starting from it), except the specific one from the $M_{m,r}$ class, to other mutants. The death and replacement events have already happened and we are looking for the probability that a random edge that goes from a mutant to another mutant is an edge that connects the replaced mutant to a mutant from the $M_{m,r}$ class. This edge obviously cannot be any of the m edges of that individual.

By symmetric arguments, the probability that an individual leaves the $R_{m,r}$ class and enters the $R_{m+1,r-1}$ class is given by

$$\sum_{k=1}^{D_{\max}} \sum_{i+j=k} (R_{i,j} - \delta_{mr}^{ij}) \frac{\frac{1}{(i\gamma+j\delta)/(i+j)}}{\overline{F}} \cdot \frac{i}{i+j} \cdot \frac{jr}{\sum\limits_{k=1}^{D_{\max}} \sum\limits_{i+j=k} jR_{i,j} - r} = \frac{H_2 r}{\overline{F}(L_{\mathrm{RR}} - r)}, \tag{4.22}$$

while the probability of leaving the $R_{m,r}$ class and moving to the $R_{m-1,r+1}$ class is given by

$$\sum_{k=1}^{D_{\max}} \sum_{i+j=k} M_{i,j} \frac{\frac{1}{(i\alpha+j\beta)/(i+j)}}{\overline{F}} \cdot \frac{j}{i+j} \cdot \frac{jm}{\sum\limits_{k=1}^{D_{\max}} \sum\limits_{i+j=k} jM_{i,j}} = \frac{H_4 m}{\overline{F} L_{\mathrm{MR}}}. \tag{4.23}$$

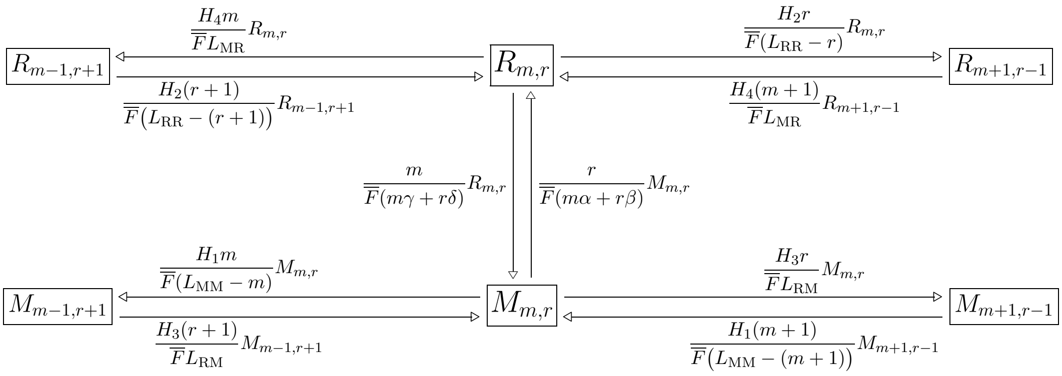


Figure 4.1: Diagram showing all the probabilities of transition from and to the classes $M_{m,r}$ and $R_{m,r}$.

The transition probabilities of moving from and to the $M_{m,r}$ and $R_{m,r}$ classes are represented schematically in the diagram in Figure 4.1

The dynamics of the $D_{\max}(D_{\max}+3)$ different classes of the population is described by the following differential equation based compartmental model

$$\begin{aligned}\dot{M}_{m,r} = &-\frac{1}{\overline{F}}\left(\frac{H_3 r}{L_{\mathrm{RM}}}+\frac{H_1 m}{L_{\mathrm{MM}}-m}+\frac{r}{m\alpha+r\beta}\right)M_{m,r}+\frac{H_1(m+1)}{\overline{F}\big(L_{\mathrm{MM}}-(m+1)\big)}M_{m+1,r-1}\\ &+\frac{H_3(r+1)}{\overline{F}L_{\mathrm{RM}}}M_{m-1,r+1}+\frac{m}{\overline{F}(m\gamma+r\delta)}R_{m,r}, \qquad (4.24)\\ \dot{R}_{m,r} = &-\frac{1}{\overline{F}}\left(\frac{H_2 r}{L_{\mathrm{RR}}-r}+\frac{H_4 m}{L_{\mathrm{MR}}}+\frac{m}{m\gamma+r\delta}\right)R_{m,r}+\frac{H_4(m+1)}{\overline{F}L_{\mathrm{MR}}}R_{m+1,r-1}\\ &+\frac{H_2(r+1)}{\overline{F}\big(L_{\mathrm{RR}}-(r+1)\big)}R_{m-1,r+1}+\frac{r}{\overline{F}(m\alpha+r\beta)}M_{m,r}, \qquad (4.25)\end{aligned}$$

for $\{(m,r): m\geq 0, r\geq 0, 1\leq m+r\leq D_{\max}\}$.

The density of As in the population is given by $p_A=\sum_{k=1}^{D_{\max}}\sum_{m+r=k}M_{mr}/N$, and the density of Bs by $p_B=\sum_{k=1}^{D_{\max}}\sum_{m+r=k}R_{mr}/N$.

Note that for very large population sizes, the subtractions of m and $m+1$ from L_{MM}, and r and $r+1$ from L_{RR} as well as those of δ_{mr}^{ij} in the terms H_1 and H_2, in the model (4.24)–(4.25), can be omitted since their effect is negligible (see for example Lindquist *et al.* (2011) and Gleeson (2011) where in models of a similar nature such subtractions are avoided). However, this would reduce the accuracy of the solution of the model when the population size is small. Moreover, it should be mentioned that the above subtractions might result in negative values of $M_{m,r}$ and/or $R_{m,r}$ for some values of m and r. This is due to the fact that the numerical solution of the system might lead to non-integer values of these quantities which lie between 0 and 1. As a result, the terms $L_{\mathrm{MM}}-m$, $L_{\mathrm{MM}}-(m+1)$, $L_{\mathrm{RR}}-r$ and $L_{\mathrm{RR}}-(r+1)$ might become negative. This problem can be solved by setting these terms to be bounded below by 1, which is the minimum natural value that these terms can take.

4.2.3 Numerical examples and comparisons with stochastic simulations

In this section, we examine the effectiveness of the two approximation models described in Sections 4.2.1 and 4.2.2; the pairwise model and the Neighbourhood Configuration model. As specific examples we consider the evolution of the population when individuals play Hawk–Dove type games (see Section 2.6.2) (Maynard Smith and Price, 1973; Maynard Smith, 1982).

We consider Hawk–Dove type games played on three commonly used families of graphs; the random regular graphs, the random graphs and the scale-free networks. The random graph we consider is an Erdős–Rényi type random graph (Erdős and Rényi, 1959) generated as described in Lindquist *et al*. (2011). Assume a population of N vertices with no connections between them. Firstly, every (non-connected) vertex is connected to a random vertex with degree less than the maximum allowable degree $D_{\max}$. In order to ensure that the graph will be connected (there will be a path between every two vertices of the graph), initially a pair of vertices is connected, and then each of the remaining (non-connected) vertices is connected to a randomly chosen vertex which is already connected, sequentially. After the connection of all the vertices, two vertices with degree less than $D_{\max}$ are chosen at random and become connected. The last step is iterated until the desired average degree of the graph, $\langle k \rangle$, is reached. The random regular graphs are generated in the same way as the random graph by assuming that $D_{\max} = k$, i.e. with the restriction that every vertex has the same number of connections. The scale-free networks are graphs that have power-law (or scale-free) degree distributions. These are generated following the algorithm of preferential attachment (Barabási and Albert, 1999; Albert and Barabási, 2002). The initial graph consists of a small number of m_0 vertices connected with l_0 edges. A new vertex of degree equal to m ($\leq m_0$) is added to the graph and each of its edges is connected to one of the existing vertices. The probability that one of the m edges is connected to vertex i with degree k_i is equal to $k_i / \sum_{j=1}^{N} k_j$ (preferential attachment). This process is repeated until the network is composed of N vertices. Given that this happens after $t = N - m_0$ iteration steps, the number of new edges that will be added in the graph will be equal to mt. Therefore, the network obtained has average degree equal to $\langle k \rangle = 2(mt + l_0)/N$, which for sufficiently large N is well approximated by $2m$. Note that in all the graphs we consider, it is assumed that

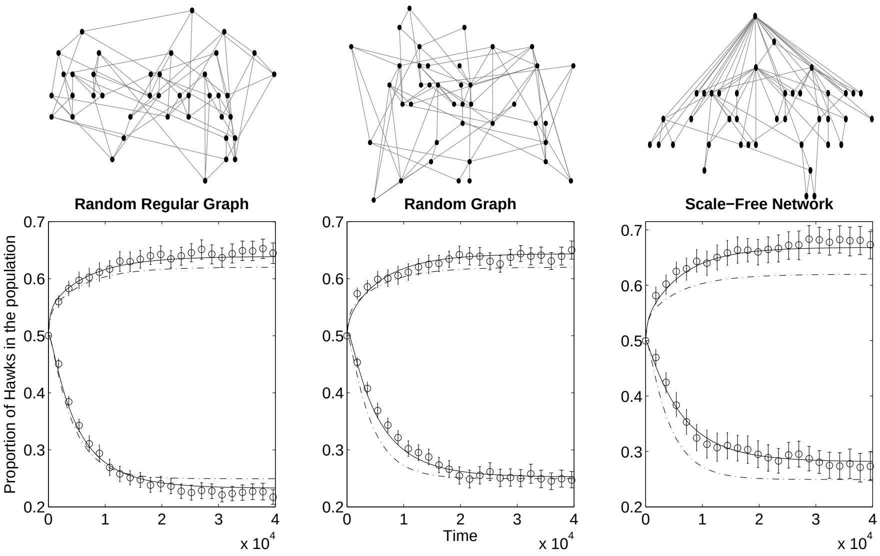


Figure 4.2: Change over time in the proportion of individuals playing the Hawk strategy in a Hawk–Dove game played on a random regular graph with $k = 4$, a random graph with $\langle k \rangle = 4$ and $D_{\max} = 10$, and a scale-free network with $\langle k \rangle = 4$. The solid lines represent the solution of the Neighbourhood Configuration model, the dashed-dotted lines represent the solution of the pairwise model, and the circles represent the average of 100 stochastic simulations. A 95% bootstrap confidence interval for the mean of the simulation results is also presented. The upper curves of each sub-figure represent the case of a game described by the payoff matrix (1.19) where $V = 6$, $C = 10$, $f_b = 4$ and $w = 1$. The lower curves represent the case of a game where $V = 4$, $C = 10$, $f_b = 4$ and $w = 1$.

the edges between vertices are undirected, every two vertices are connected with at most one edge and there are no self-loops.

In all the examples, it is assumed that at the initial state of the process the population consists of 50% of individuals playing the Dove strategy and 50% of individuals playing the Hawk strategy, randomly distributed among the vertices of the graph, so that there is no initial advantage to either of the strategies. The population size, N, is relatively small, $N = 400$. The results of the pairwise model and the Neighbourhood Configuration model are compared with the average of 100 different network realisations. The equilibrium densities of the strategies have been obtained by averaging the frequency over the last 5000 iteration steps in 40000 iteration steps (for each graph convergence to an equilibrium state was effectively achieved at a significantly earlier time).

The numerical examples shown in Figure 4.2 indicate that, on the three types of graph we consider, the prediction of the change in the frequencies of strategies over time given by the solution of the Neighbourhood Configuration model (4.24)–(4.25) agrees very well with the results of computer simulations. The numerical results also indicate that the more detailed model provides an approximation with improved ac-

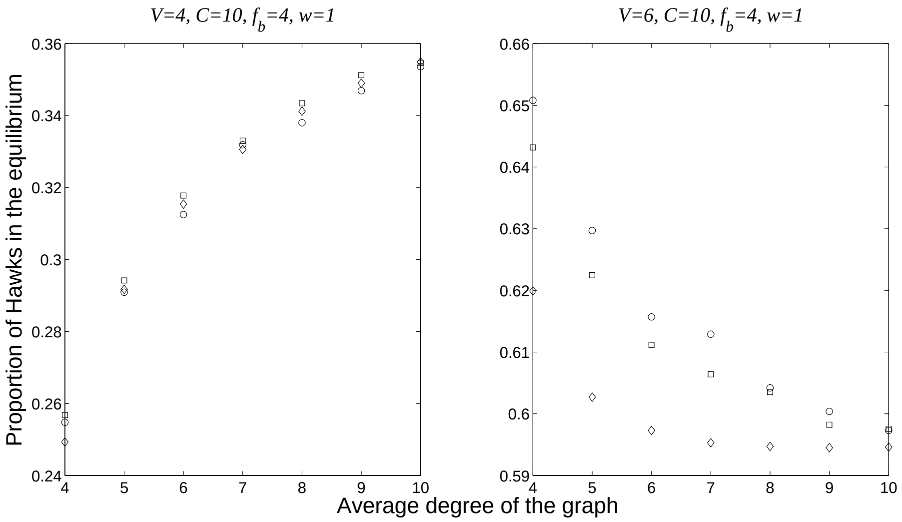


Figure 4.3: The proportion of Hawks in the equilibrium on random graphs of different average degree, $\langle k \rangle$. The maximum degree of a vertex, D_{max}, in each of the graphs is equal to $\langle k \rangle + 6$. The squares represent the solution of the Neighbourhood Configuration model, the diamonds represent the solution of the pairwise model, and the circles represent the average of 100 stochastic simulations.

curacy compared to the solution of the pairwise model. Although it is observed that contact structure has little effect on such evolutionary dynamics, the effectiveness of the Neighbourhood Configuration model is clearer on heterogeneous graphs and in general on graphs of low degree, when compared with the pairwise model. As the average degree of the graph increases, i.e. the homogeneity of the graph increases, the predictions of both models are in good agreement with simulation results (see for example, Figure 4.3).

Although the aim of this chapter is to present this powerful approximation method for the approximation of the evolutionary game dynamics in structured populations, let us consider some main conclusions about the effect of the population structure on the outcome of the evolutionary dynamics in a Hawk–Dove game. Specifically, we discuss how the Hawk and Dove strategies spread in a population represented by a random regular graph, a random graph and a scale-free network. Numerical examples suggest that increasing the heterogeneity of the graph favours the emergence of the Hawk strategy. Following the update rules of the VM, fitter mutants that occupy vertices of high connectivity have an increased chance to survive and reproduce (Sood *et al.*, 2008; Hadjichrysanthou *et al.*, 2011). Therefore, as is observed in Figure 4.2, scale-free networks provide an encouraging environment for the Hawk strategy. However, the most important feature of a graph that affects the evolutionary process is its average degree. The results of our examples indicate that in all types of graph we consider, a decrease of the average number of neighbours that each individual has tends to deviate the equilibrium frequency of Hawks from the equilibrium frequency in the case of the well-mixed population, and this deviation is more pronounced for lower degree graphs. Depending on the values of the payoffs, the decrease of the average degree of the neighbours might enhance or inhibit the use of the Hawk strategy (and thus the Dove strategy). In particular, if the payoffs are such that the equilibrium frequency of Hawks in a well-mixed population is less than half of the population, the decrease of the average number of neighbours decreases their frequency at equilibrium conditions (at least when the average degree is already sufficiently small). If the payoffs are such that the equilibrium frequency in a well-mixed population is higher than half, the equilibrium frequency will tend to increase as the average number of neighbours decreases (see in Figure 4.3 the effect of the variation of the average degree of a random graph in two example games). Note that the improved approximation of the Neighbourhood Configuration model when compared to that of the pairwise model is not very clear in our examples presented in Figure 4.3, mainly due to the particular example games and the graphs on which the games are played. However, the scope of this figure is to illustrate the effect of the average connectivity of the graph at the equilibrium state of the system.

It should be noted that, due to the nature of the evolutionary dynamics as well as to the nature of the game we consider, the evolution of the population is very slow, especially for graphs of low connectivity, and to speed up the evolutionary process and reduce the computation time, we reduce the population size and the number of simulations realised. However, small population sizes and small number of realisations of stochastic simulations result in larger oscillations of the simulation results due to the increase of the sensitivity of the process to stochastic effects. Increasing the population size and the number of realisations, this effect is reduced and the difference between the predictions of the computer simulations and the predictions of the Neighbourhood Configuration model decreases.

4.3 Discussion

In this work, we have investigated the stochastic evolutionary game dynamics in structured populations following the update rules of the VM dynamics, a dynamics which is applied in many models that arise in various fields. Whilst analytic investigation of this dynamics is possible when populations have a simple structure, the study of the dynamics in complex structures requires the use of approximation techniques. Here, we propose a Neighbourhood Configuration model for the study of the stochastic evolutionary dynamics of a two-strategy game on complex graphs. This modelling framework offers a flexible way to carry out a systematic analysis of evolutionary game dynamics on graphs and to establish the link between network topology and potential system behaviours.

As an example, we have considered a Hawk–Dove game played in three widely used types of graph; random regular graphs, random graphs and scale-free networks. The solutions of the model constructed in comparison with the outcome of stochastic simulations imply that the method followed is a powerful and effective method for the approximation of such evolutionary processes. In addition, comparisons with the results of the extensively used pairwise approximation suggest that this method improves the accuracy of the approximation solutions.

Although the aim of this chapter is the introduction of the Neighbourhood Configuration model for the approximation of evolutionary game dynamics on graphs, we have considered some important characteristics of the graph that might affect the evolution of a population when a Hawk–Dove game is played among individuals. The spatial effects in this evolutionary game have received considerable attention in many previous works, including Killingback and Doebeli (1996), Hauert and Doebeli (2004), Tomassini *et al.* (2006), Broom *et al.* (2010a), Voelkl (2010) and Hadjichrysanthou *et al.* (2011). One of the main research questions is whether there are structures and strategy update rules which favour the persistence of the cooperative Dove-like behaviour over the Hawk-like behaviour compared to the evolution in classical evolutionary game theory under the assumption that the population is well-mixed and infinitely large. Killingback and Doebeli (1996) have shown that, for a wide range of parameter values, the square lattice structure may favour the Dove strategy, with respect to the equilibrium frequency of Doves in the population compared to the equilibrium frequency in the classical Hawk–Dove game. On the other hand, in Hauert and Doebeli (2004), extending the investigation of the evolution in this type of game to a broader class of lattices and under different strategy update rules, the authors concluded that spatial structure usually does not promote the evolution of the Dove strategy. Santos and Pacheco (2005) showed that among other structures, in Hawk–Dove type games (specifically, in the Snowdrift game), under some specific strategy update rules, the evolution of the Dove-like (cooperative) strategies are facilitated particularly on scale-free networks due to the existence of highly connected Doves (see also Santos *et al.*, 2006a). Tomassini *et al.* (2006), based on the results of computer simulations, have considered the game played among individuals on lattices, random graphs and small-world networks and shown that, compared with the case of the well-mixed population, these types of network might enhance or inhibit the use of the Dove strategy (the proportion of Doves at the equilibrium state might be either higher or lower than their proportion given by the theoretical solution of the classical evolutionary game theory), depending on the update rule and the ratio V/C. In Broom *et al.* (2010a), Voelkl (2010) and Hadjichrysanthou *et al.* (2011) it has been shown through an analytical and numerical investigation that the Dove behaviour is favoured on some structures with respect to the probability and time to fixation. In this chapter, through numerical examples we have shown that the population structure might significantly influence the evolution of the population. The most important feature of the graph that affects evolution in our examples seems to be average connectivity. Decreasing the average number of connections of each individual increases the difference between the proportion of Hawks from their proportion in the equivalent infinite homogeneous well-mixed population, in the direction of the nearest absorption state. Hence, depending on the values of the payoffs, the decrease of the average connectivity of the graph enhances or inhibits the use of the Hawk strategy. In addition, heterogeneous graphs have been shown to facilitate the spread of Hawks. Particularly, the existence of highly connected vertices promotes the Hawk strategy and scale-free networks appear to be the most hospitable environment among the graphs we have considered.

The approximation method presented in this chapter is undoubtedly a useful tool which provides an effective way to consider evolutionary dynamics on a wide range of graphs. We believe that its use in future research could give insight into the influence of the population structure on the outcome of such dynamics (see Gleeson, 2011). Future work could involve the application of the Neighbourhood Configuration model in the investigation of other type of dynamics, for example birth-death dynamics where the birth event happens first followed by the death and replacement events. One extension of the model could be the inclusion of a mutation process, a process that usually occurs in natural systems. For example, it could be assumed that with a certain probability the offspring of an X individual is not a copy of its parent but is a Y individual. This would add some complication in the model, because in this case an X might be replaced by a Y, which is the offspring of a neighbouring X individual. Such an extension would allow us to consider the effect of mutation on evolution on graphs, an important factor that has rarely been studied. This method is also amenable to be extended to dynamic graphs and thus offer further potential advantages to modellers (see a modelling framework in this direction in the context of disease propagation in Marceau *et al.* (2010) and Taylor *et al.* (2012)).

CHAPTER 5

Models of kleptoparasitism on graphs

5.1 Introduction

The game-theoretical model of Broom and Ruxton (1998) on the evolution of kleptoparasitic populations (see Section 1.6), as well as a large amount of work which has followed based on this model, assumed that the population of foraging animals is an infinitely large and well-mixed population where every animal is equally likely to meet any other animal. However, in natural situations, animals usually forage in small groups forming some complex relationships and social structure (e.g., Krause *et al.*, 2007; Croft *et al.*, 2008). A number of stochastic models have been developed to consider the evolution of kleptoparasitic populations of finite size (see Yates and Broom, 2007; Crowe *et al.*, 2009). Moreover, the effect of the structure of such populations on the evolutionary process remains a significant research question.

In this chapter, we explore the role of the population structure in the evolution of kleptoparasitic populations. We extend the original model of Broom and Ruxton (1998) by assuming that animals occupy the vertices of a static graph. First, we consider a regular graph, i.e. the case where each animal of the population has an equal number of connections. Then, we examine the evolution of the population when animals have more complex structures represented by a random graph or a scale-free network.

5.2 Models of kleptoparasitism on random regular graphs – The pair approximation model

In this section, we consider the basic model of Broom and Ruxton (1998) (also discussed in Section 1.6) assuming that the animals of the population occupy the vertices of a regular graph.

In order to consider the dynamics of a population of which individuals are placed on a regular graph, we use the pair approximation method (Matsuda *et al.*, 1992; van Baalen and Rand, 1998; Keeling, 1999; Eames and Keeling, 2002; House and Keeling, 2011, see also Section 4.2.1).

Assume that animals of a finite population occupy the vertices of a regular graph of degree k, i.e. every animal has exactly k neighbours. Let $[X]$ be the number of animals in state X, $[XY]$ the number of pairs between an animal in state X and an animal in state Y, $X-Y$, and $[XYZ]$ the number of triples of type $X-Y-Z$. X, Y, and Z represent any of the states that an animal can be in; the searching state S, the handling state H and the fighting state F. Note that two connected animals in the fighting state F might fight each other or they might fight with another animal. We distinguish these different types of pairs of animals in the fighting state by denoting by $[FF_j]$ the number of pairs of animals which are fighting each other, F_j-F_j, and by $[FF]$ the number of pairs of animals which are involved in a fight but are not fighting each other, $F-F$.

The total population size, P, is assumed to be constant and so

$$[S]+[H]+[F]=P. \tag{5.1}$$

Note that $X-X$ pairs are counted twice (once in each direction, and thus $[XX]$ is always even) while $X-Y$ pairs are counted once in each direction. There are 10 distinct pairs. However, due to the fact that $[XY]=[YX]$ and that

$$[SS]+[HH]+[FF]+[FF_j]+2[SH]+2[SF]+2[HF]=kP, \tag{5.2}$$

the dynamics of the 10 pairs, can be described by the dynamics of only 6 pairs.

As in the original model, the animals in the searching state S change to the handling state H at rate $\nu_f f$, where the time units depend on the animal species, but they are usually seconds or minutes (see for example, Hockey *et al.*, 1989). Thus, at the same rate, $S-S$, $S-H$ and $S-F$ pairs become $S-H$, $H-H$ and $H-F$ pairs, respectively. Single animals in state H move to state S at rate $1/t_h$ and thus, with the same rate $S-H$, $H-H$ and $H-F$ pairs become $S-S$, $S-H$ and $S-F$ pairs, respectively. A pair consisting of a searcher and a handler, $S-H$, engage in a fight at rate $p\nu_h$. Hence, at rate $p\nu_h$, pairs $S-H$ become F_j-F_j. Thus, $p\nu_h[SH]$ single animals in state S and $p\nu_h[SH]$ single animals in state H move to state F. If $S-H$ pairs are connected to an animal already involved in a fight, F, then the triples $F-S-H$ and $F-H-S$ become $F-F_j-F_j$, both at rate $p\nu_h$. Hence, $S-F$ and $H-F$ pairs become $F-F$ pairs at rates $p\nu_h[FSH]$ and $p\nu_h[FHS]$, respectively. If an $S-H$ pair engage in a fight and this pair is connected to either an animal S or an animal H such that $S-H-S$ or $H-S-H$ triples exist, then $S-F$ and $H-F$ pairs, respectively, will be generated while $S-H$ pairs will be reduced. Therefore, the number of $S-F$ and $H-F$ pairs is increased with rate $p\nu_h[SHS]$ and $p\nu_h[HSH]$, respectively, while the number of $S-H$ pairs is decreased with rate $p\nu_h([SHS]+[HSH])$. Similarly, if an $S-H$ pair is connected to an S in a way a triple $S-S-H$ exists, then the $S-S$ pairs become $S-F$ pairs at rate $p\nu_h[SSH]$. By symmetry, $H-H$ pairs become $H-F$ pairs at rate $p\nu_h[HHS]$. Fights end at rate $2/t_a$ and therefore with this rate pairs of animals leave the fighting state F. Half of them move to the S state and half of them move to the H state. With this rate, F_j-F_j pairs become $S-H$ pairs as well. The pairs of animals which consist of at least one animal involved in a fight, i.e. the $S-F$, $H-F$ and $F-F$ pairs also become $S-H$ and $S-S$, $H-S$ and $H-H$, and $S-F$ and $H-F$ pairs with rate $1/t_a$, respectively (with probability 0.5 the animal in state F of each of the pairs will be either the winner or the loser of the fight).

According to the above, the dynamics of the different singles and pairs can be described by the following system of differential equations

$$\frac{d[S]}{dt} = \frac{1}{t_h}[H] + \frac{1}{t_a}[F] - \nu_f f[S] - p\nu_h[SH], \tag{5.3}$$

$$\frac{d[H]}{dt} = \nu_f f[S] + \frac{1}{t_a}[F] - \frac{1}{t_h}[H] - p\nu_h[SH], \tag{5.4}$$

$$\frac{d[F]}{dt} = 2p\nu_h[SH] - \frac{2}{t_a}[F], \tag{5.5}$$

$$\frac{d[SS]}{dt} = \frac{2}{t_h}[SH] + \frac{2}{t_a}[SF] - 2\nu_f f[SS] - 2p\nu_h[SSH], \tag{5.6}$$

$$\frac{d[HH]}{dt} = 2\nu_f f[SH] + \frac{2}{t_a}[HF] - \frac{2}{t_h}[HH] - 2p\nu_h[HHS], \tag{5.7}$$

$$\frac{d[FF]}{dt} = 2p\nu_h\left([FSH]+[FHS]\right) - \frac{4}{t_a}[FF], \tag{5.8}$$

$$\frac{d[FF_j]}{dt} = 2p\nu_h[SH] - \frac{2}{t_a}[FF_j], \tag{5.9}$$

$$\begin{aligned}\frac{d[SH]}{dt} &= \nu_f f[SS] + \frac{1}{t_h}[HH] + \frac{1}{t_a}\left([SF]+[HF]+[FF_j]\right) - \\ &\quad - \nu_f f[SH] - \frac{1}{t_h}[SH] - p\nu_h\left([SH]+[SHS]+[HSH]\right),\end{aligned} \tag{5.10}$$

$$\begin{aligned}\frac{d[SF]}{dt} &= \frac{1}{t_h}[HF] + \frac{1}{t_a}[FF] + p\nu_h\left([SHS]+[SSH]\right) - \\ &\quad - \nu_f f[SF] - \frac{2}{t_a}[SF] - p\nu_h[FSH],\end{aligned} \tag{5.11}$$

$$\frac{d[HF]}{dt} = \nu_f f[SF] + \frac{1}{t_a}[FF] + p\nu_h\left([HSH] + [HHS]\right) - \\ - \frac{1}{t_h}[HF] - \frac{2}{t_a}[HF] - p\nu_h[SHF]. \tag{5.12}$$

The number of the triples $[ABC]$ can be evaluated by using the following moment closure approximation (see for example, Keeling, 1999; Rand, 1999)

$$[ABC] = \left(\frac{k-1}{k}\right)\frac{[AB][BC]}{[B]}. \tag{5.13}$$

Note that instead of closing the system of equations at the level of pairs by approximating the triples by expressions in terms of pairs, it is possible to close the system at higher order configurations, for example at the level of triples by approximating the forth-order moments by expressions in terms of triples and thus in terms of pairs (see for example Bauch (2005) for the derivation of a triple approximation in an SIS epidemic model). This can result in a better approximation of the solution.

5.2.1 Equilibrium points

The equilibrium points of the system of equations (5.3)–(5.12) are the solutions of the system

$$\frac{d[S]}{dt} = \frac{d[H]}{dt} = \frac{d[F]}{dt} = \frac{d[SS]}{dt} = \frac{d[HH]}{dt} = \frac{d[FF]}{dt} \\ = \frac{d[FF_j]}{dt} = \frac{d[SH]}{dt} = \frac{d[SF]}{dt} = \frac{d[HF]}{dt} = 0. \tag{5.14}$$

Approximating the number of triples by the expression (5.13) and using equation (5.1) we find that at the equilibrium the number of singles is given by

$$[S] = m, \quad [H] = t_h\nu_f fm, \quad [F] = pt_ht_a\nu_f f\nu_h q, \tag{5.15}$$

and the number of the different pairs by

$$[SS] = q, \tag{5.16}$$

$$[HH] = t_h^2(\nu_f f)^2 q, \tag{5.17}$$

$$[FF] = \left(\frac{k-1}{k}\right)^2 \frac{p^2t_h^2t_a^2(\nu_f f)^2\nu_h^2q^3}{m^2}, \tag{5.18}$$

$$[FF_j] = pt_ht_a\nu_f f\nu_h q, \tag{5.19}$$

$$[SH] = t_h\nu_f fq, \tag{5.20}$$

$$[SF] = \left(\frac{k-1}{k}\right)\frac{pt_h t_a \nu_f f \nu_h q^2}{m}, \tag{5.21}$$

$$[HF] = \left(\frac{k-1}{k}\right)\frac{pt_h^2 t_a (\nu_f f)^2 \nu_h q^2}{m}. \tag{5.22}$$

We have set

$$m = \frac{P - pt_h t_a \nu_f f \nu_h q}{1 + t_h \nu_f f}, \tag{5.23}$$

and

$$q = \frac{kP\left(F \pm \sqrt{F^2 - 4pt_h t_a \nu_f f \nu_h G}\right)}{2pt_h t_a \nu_h \nu_f f G}, \tag{5.24}$$

where

$$F = t_h \nu_f f\left(2kpt_a \nu_h + t_h \nu_f f + 2\right) + 1, \tag{5.25}$$

$$G = t_h \nu_f f\left(k^2 pt_a \nu_h + t_h \nu_f f + 2\right) + 1. \tag{5.26}$$

Note that in expression (5.24), only the point where the square root is subtracted can give a biologically plausible equilibrium solution, because only then can m, in (5.23), be non-negative.

5.2.2 Effect of the degree of the graph

The decrease of the number of neighbours of each animal decreases the rate at which animals engage in fights for food. Therefore the number of animals which are either searching for food or handling a food item at each time increases (see Figure 5.1). However, it is shown that decreasing the number of neighbouring animals has almost the same effect as decreasing the rate at which foragers encounter handlers in a homogeneous well-mixed population, i.e. as decreasing ν_h. Numerical investigation has shown that when $\nu_h = 1/k$, although an increase in the density of animals in state F and that of pairs $S-S$, $H-H$, $S-H$ and $F_j - F_j$ is observed with the decrease of the degree of the graph k, as well as a decrease in the densities of S, H, $F-F$, $S-F$ and $H-F$, these changes in the densities are almost negligible (see for example Figure 5.2). A more pronounced effect of the variation of k is observed in the densities of $F-F$ and $F_j - F_j$ pairs. In the example of Figure 5.2b, the actual number of $F_j - F_j$ pairs, $[FF_j]$, decreases as k increases due to the fact that the rate at which animals engage in fights over food is inversely proportional to k (when $\nu_h = 1$ the actual number $[FF_j]$ increases as k increases but the density of $F_j - F_j$ pairs decreases as well). On the other hand, the density of $F-F$ pairs increases as k increases because the higher the number of connections of each animal, the higher

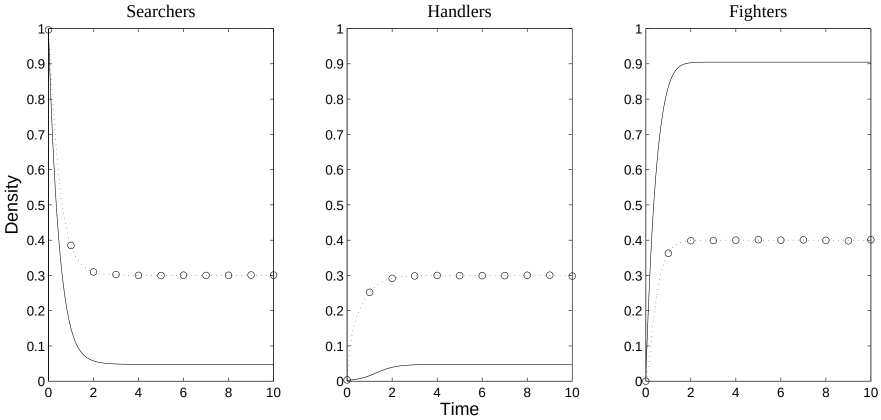
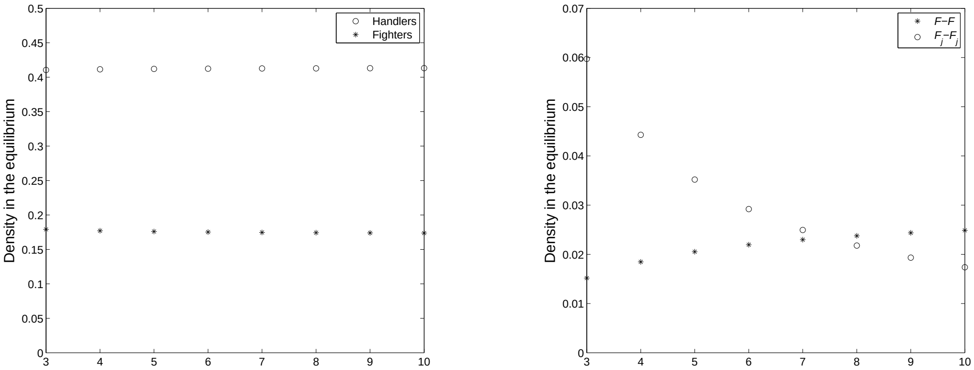


Figure 5.1: Change over time in the density of searchers (S), handlers (H) and fighters (F) on a random regular graph with $k = 4$. The circles represent the average of 1000 stochastic simulations. The respective solution in the well-mixed population is represented by the solid line. $t_a/2 = 0.5, t_h = 1, \nu_f f = 1, \nu_h = 1, p = 1, P = 1$.



a) b)

Figure 5.2: (a) The equilibrium density of handlers (H) and fighters (F), and (b) the equilibrium density of the pairs $F - F$ and $F_j - F_j$, on random regular graphs of different degree. $t_a/2 = 0.5, t_h = 1, \nu_f f = 1, \nu_h = 1/k, p = 1, P = 1$. Note that in this example the equilibrium density of searchers and that of handlers are equal.

the chance of an animal being next to another animal which is fighting.

Hence, the evolution of a kleptoparasitic population when animals are placed on a regular graph is not significantly affected compared to the evolution of the respective homogeneous well-mixed population. This is mainly due to the fact that the number of connections is the same for every animal and thus every animal has the same chance to engage in an aggressive interaction. In addition, all animals discover food items at a constant rate, independently of the population structure; obviously this reduces the effect of any population structure in general.

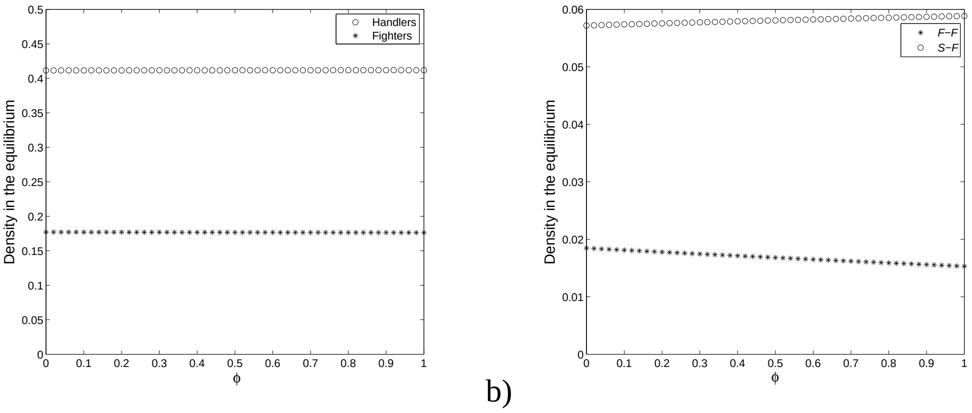
5.2.3 Clustering effect

Using the moment closure approximation (5.13) to approximate triples in terms of pairs, we ignore the actual structure of the graph. For example, using (5.13), we count the triples as three vertices connected in a line ignoring the fact that the three vertices might form a loop. For instance, in a triple where a B individual is connected to an A individual and a C individual, A can also be connected to C. The most commonly used method to take into consideration such triangular loops, is to use the following closure approximation (see Keeling, 1999):

$$[ABC] = \frac{(k-1)}{k}\frac{[AB][BC]}{[B]}\left(1-\phi+\phi\frac{N}{k}\frac{[AC]}{[A][C]}\right). \tag{5.27}$$

ϕ is defined as the ratio of the number of triangles to the number of connected triples and is usually called the *clustering coefficient*. When ϕ is small, paired individuals are more likely to have different neighbours while when ϕ is large many of the neighbours of two connected individuals will be common. For $\phi = 0$ this approximation is equivalent to (5.13). Similar approximations can be constructed for larger loops, e.g. squares. However, the effect of loops of higher than three vertices will be much less than the effect of the loops of three vertices.

Considering the effect of the ratio ϕ on the dynamics of kleptoparasitic populations described by the system of equations (5.3)–(5.12), it is shown that the variation of ϕ does not greatly affect the dynamics of the different groups. As ϕ increases, a small decrease is observed in the density of the subpopulation of fighters, and thus the density of searchers and handlers increases (see Figure 5.3a for an example). One reason for this is that a searcher in a triple $S-H-S$ or a handler in a triple $H-S-H$ are less likely to fight if the triples form a triangle, i.e. if the two searchers of the first triple and the two handlers of the second triple are also connected. The number of all of the pairs of animals in the different states, apart from the $S-F$ and $H-F$ pairs, decreases with the increase of ϕ, with the number of $F-F$ pairs being the most affected (see Figure 5.3b) due to the fact that the chance of a searcher or a handler being involved in a fight reduces when this forms a triangle with an F_j-F_j pair. The number of $S-F$ and $H-F$ pairs increases (see Figure 5.3b). This is mainly due to effect of the fact that when a fight takes place between $S-H$ pairs which are connected to a searcher or a handler animal X, such as triples $X-H-S$ and $X-S-H$ exist, then two $X-F$ pairs are created if those triples form a triangle, i.e. when X and S, and X and H, respectively, are also connected. At the same time, as mentioned above, the chance of animal X engaging in a fight in this case decreases. Thus, the number of $X-F$ pairs increases. The number of the pairs



a) b)

Figure 5.3: (a) The equilibrium density of handlers (H) and fighters (F), and (b) the equilibrium density of the pairs $F-F$ and $S-F$, on a random regular graph of degree $k=4$ as the ratio ϕ varies. $t_a/2=0.5, t_h=1, \nu_f f=1, \nu_h=1/k, p=1, P=1$. Note that in this example the equilibrium density of searchers and that of handlers are equal.

$S-F$ and $H-F$ is the most affected by the variation of ϕ after the number of $F-F$ pairs. Note that as the connectivity of the graph increases, the above effect of the ratio ϕ decreases even more.

5.3 Models of kleptoparasitism on random graphs and scale-free networks

In the previous section, it has been shown that in homogeneous well-mixed kleptoparasitic populations described by the model of Broom and Ruxton (1998), the decrease of the number of connections of each animal and the change of the actual structure of the population does not significantly affect the evolution of the population, given that this decrease is the same for every animal. However, numerical investigations show that evolution might be affected if the animals are placed on degree-heterogeneous graphs and this effect becomes more pronounced when the heterogeneity of the graph increases.

Figure 5.4 and Figure 5.5 show the variation in the density of searchers, handlers and fighters over time when the structure of the population is represented by a random graph and a scale-free network, respectively (see Section 4.2.3 for a description and instructions for the construction of these graphs). Although the effect on the density of the three subpopulations is not clear when the population structure is represented by a random graph with low-degree heterogeneity, there is a pronounced effect when the population structure has the features of a scale-free network. The existence of highly connected animals reduces the number of fights taking place

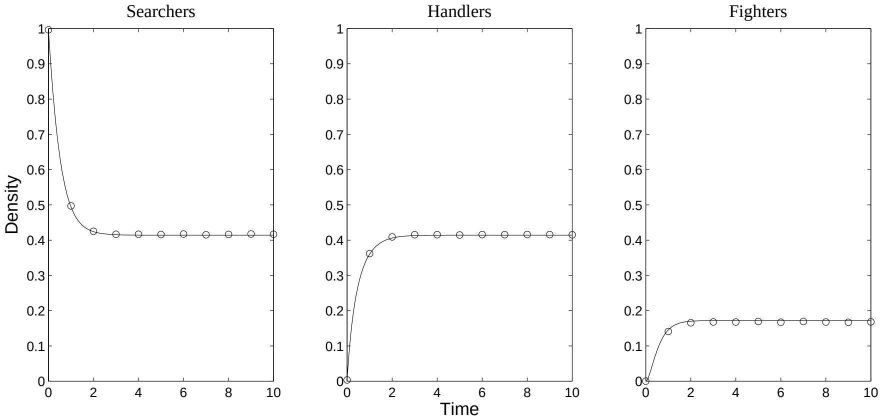


Figure 5.4: Change over time in the density of searchers (S), handlers (H) and fighters (F) on a random graph with average degree $\langle k \rangle = 4$ and maximum degree of a vertex equal to 12. The circles represent the average of 1000 stochastic simulations. The respective solution in the well-mixed population is represented by the solid line. $t_a/2 = 0.5, t_h = 1, \nu_f f = 1, \nu_h = 1/\langle k \rangle, p = 1, P = 1$.

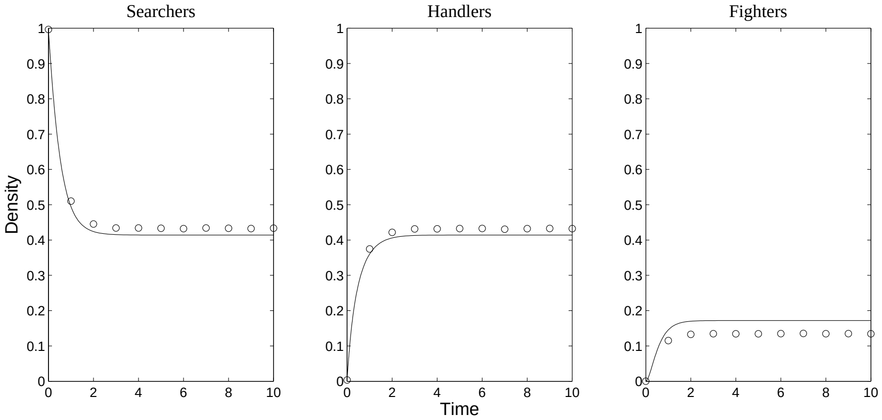


Figure 5.5: Change over time in the density of searchers (S), handlers (H) and fighters (F) on a scale-free network with average degree $\langle k \rangle = 4$. The circles represent the average of 1000 stochastic simulations. The respective solution in the well-mixed population is represented by the solid line. $t_a/2 = 0.5, t_h = 1, \nu_f f = 1, \nu_h = 1/\langle k \rangle, p = 1, P = 1$.

over food and thus the number of animals searching for food or handling a food item increases. This is due to the fact that the lowly connected animals placed on a scale-free network that are linked with a highly connected animal have a very small (or even zero) chance to interact aggressively, either as attacking searchers or attacked handlers, especially in the case where the highly connected animal is already involved in a fight. This has a direct consequence on the food consumption of animals with high connectivity. The higher the number of connections of an animal, the higher its chance of attacking a neighbouring animal as a searcher or being attacked by other animals as a handler. Thus, animals with high connectivity most of

Table 5.1: The equilibrium proportion of searchers, handlers and fighters that occupy vertices of degree d in a scale-free network with maximum degree D_{max}. Recall that the degree distribution of a scale-free network follows a power law, and thus such graphs have few large degree vertices and many small degree vertices. The results presented are the average of 200 simulations. $t_a/2 = 0.5, t_h = 1, \nu_f f = 1, \nu_h = 1/\langle k \rangle, p = 1, P = 1$. The foraging time is equal to 100. Note that the average food intake rate of the population placed on a scale-free network is equal to 0.4321 and is higher than the intake rate of the infinite well-mixed population described by the model of Broom and Ruxton (1998), which is equal to 0.4142

	Degree of the vertices, d				
	$1 \le d \le \frac{1}{5}D_{\max}$	$\frac{1}{5}D_{\max} < d \le \frac{2}{5}D_{\max}$	$\frac{2}{5}D_{\max} < d \le \frac{3}{5}D_{\max}$	$\frac{3}{5}D_{\max} < d \le \frac{4}{5}D_{\max}$	$\frac{4}{5}D_{\max} < d \le D_{\max}$
Proportion of Searchers	0.4394	0.2308	0.1850	0.1500	0.0500
Proportion of Handlers	0.4421	0.2258	0.1650	0.1450	0.0550
Proportion of Fighters	0.1185	0.5433	0.6500	0.7550	0.8450
Per capita food consumption	0.4383	0.2260	0.1691	0.1188	0.0892

the time fight over food with another animal resulting in the reduction of their food consumption rate.

Table 5.1 shows how the animals in the searching, handling and fighting states are distributed over the vertices of different degree in a scale-free network when the system reaches an equilibrium state in a simulation model, as well as the per capita consumption of food items for those animals. Note that although the increase of the heterogeneity of a graph results in the decrease of the handling ratio of animals at highly connected vertices, the average handling ratio, and thus the food intake rate of the population, increases compared to that of the respective well-mixed population of the same size, or the infinite homogeneous well-mixed population of the model of Broom and Ruxton (1998). This is because, increasing the degree of heterogeneity of the graph, the number of highly connected vertices decreases and thus, the number of less connected vertices increases. Many of the animals in the poorly connected vertices have a common connected animal which most of the time fights with one of them. Hence, the other animals can search, find and consume food with a very small risk of being engaged in an aggressive interaction.

The average food intake rate calculated from the simulation model is equal to 0.4321. This is smaller than the intake rate predicted by the formula (1.42) of Broom and Ruxton (1998). The formula predicts an intake rate equal to 0.4358. This discrepancy is attributed to the fact that the intake rate given by (1.42) is calculated under the assumption that the population reaches an equilibrium state in a relatively short time, which is ignored because this is negligible compared to the total foraging period of the population. Luther and Broom (2004) have proved later that the assumption made is reasonable, at least for realistic ecological parameters. A short foraging period in the simulation model enhances the importance of the initial period of evolution before convergence to equilibrium and might result in a noticeable reduction of the value of the average intake rate. In general, the speed at which the equilibrium state is reached is very important. Some animal populations have limited foraging periods and under some ecological conditions (e.g., rare food items and high handling times) the converge to the equilibrium state might be very slow compared to these periods.

5.3.1 The simulation model

In this chapter, we simulated the evolution of kleptoparasitic populations, as described by the simple model (1.39)–(1.41) of Broom and Ruxton (1998) (see Section 1.6), on graphs. Initially, all animals are at the searching state. In a small time interval $\delta t < 0.01$, an animal in the searching state discovers a food item, independently of the graph structure, with probability $1 - \exp(-\nu_f f \delta t)$ (i.e. the number of food-discoveries in the time interval δt is assumed to follow a Poisson distribution with associated parameter $\nu_f f \delta t$). Similarly, in the interval δt, a handler animal consumes a food item with probability $1 - \exp(-t_h^{-1} \delta t)$. The probability of a searcher being engaged in a fight depends on the number of neighbouring animals handling a food item, k_H. This is taken to be equal to $1 - \exp(-k_H \nu_h \delta t)$. Similarly, the probability of a handler being discovered by a searcher and engaged in a fight is equal to $1 - \exp(-k_S \nu_h \delta t)$, where k_S is the number of the neighbouring animals of the handler searching for food. Equivalently, a searcher (handler) is engaged in a fight with every neighbouring handler (searcher) with probability $1 - \exp(-\nu_h \delta t)$. A fight ends with probability $1 - \exp(-(2/t_a)\delta t)$, and each of the animals obtains the food with probability 0.5.

5.4 Discussion

In this chapter, we have considered the original model of kleptoparasitism proposed by Broom and Ruxton (1998) in finite structured populations. The structure of the population is represented by a graph. Using the pair approximation method, we first constructed a model in order to study the evolution of the population in the case where every animal has an equal number of neighbours, that is, in the case where the population can be represented by a random regular graph. Then, using numerical simulations, we examined the evolution of kleptoparasitic populations on degree-heterogeneous graphs, such as random graphs and scale-free networks.

It has been shown that, in general, the population structure does not greatly affect the evolution of the population, mainly due to the fact that animals can discover items of food independently of the population structure. The only effect of the structure is caused due to the change of the rate at which each animal is involved in aggressive interactions. In particular, in regular graphs with lower degree the proportion of fights will be less and therefore the proportion of animals searching or handling a food item will be higher. This is due to the decreased number of neighbours of each animal and thus the decreased rate at which each animal is engaged in a fight. Moreover, since the population remains homogeneous, in the sense that every animal is exactly the same, the effect of the decrease of the degree of a regular graph has almost the same effect as that of the decrease of the rate at which animals meet each other in a homogeneous well-mixed population.

A more important influence of the population structure on the evolution of kleptoparasitic populations was observed on degree-heterogeneous structures, where the chance of being engaged in a fight, either as a searcher or a handler, is not the same for every animal in the population, due to the different degree of connectivity of animals. Especially in scale-free networks, where the variance in the degree distribution is high, the effect of the structure is more pronounced. It has been shown that, due to the fact that highly connected animals are more likely to fight over food with a neighbouring animal, the higher the connectivity of an animal the worse for the animal with respect to the consumption of food. On the other hand, poorly connected animals handling a food item have a higher chance of consuming the food before being challenged by other animals. This results in the increase of their food intake rate.

Although highly connected animals do worse than poorly connected animals on scale-free type networks, such animals are few. Hence, the number of aggressive interactions among animals on such structures are fewer than those in a well-mixed population. Consequently, the number of animals searching or handling a food item at any time is higher, and thus the average intake rate of the population is higher than the respective rate in a well-mixed population.

It would be of interest to explore further the effect of the population structure on the foraging efficiency of animals in kleptoparasitic populations, and populations in general where animals interact with each other for their survival. In nature, within a population of foraging animals, animals might use different strategies to obtain food. For example, some animals might attempt to steal food from animals of the same species (intraspecific kleptoparasitism), some others might attempt to steal food from animals of different species (interspecific kleptoparasitism), some might attempt to steal from other animals no matter if these are of the same species or different, or they might avoid any aggressive interactions. The study of the evolution of structured populations of different species of animals that use different foraging strategies would be interesting. In a stochastic process describing the evolution of a finite population, evolution will eventually lead to the dominance of one strategy for every species of animal. Moreover, in some cases strategies might coexist for a long time before the fixation of one of them. However, in a deterministic process, under some conditions, some strategies could coexist by forming clusters of animals playing the same strategy on specific parts of a graph where for example the connectivity of the vertices is high or low. In addition, an extension would be the study of such evolutionary processes on graphs where food items are not homogeneously distributed but the density of some items in some areas is higher than the density in other areas, as happens in natural systems. Although it is expected that, in general, there will be less aggressive behaviours in areas with a higher density of food items, how the different strategies are distributed on different graphs under different ecological conditions is a research question.

CHAPTER 6

Food sharing in kleptoparasitic populations

6.1 Introduction

Animals adopt varied foraging tactics in order to survive. In many biological situations, animals decide to share their food to avoid any injuries or energetic and time costs of a possible conflict with an attacking foraging animal, or to obtain other immediate or delayed benefits such as mating opportunities and reciprocal altruism. Food sharing is commonly observed in animal populations in a wide range of species, including social carnivores, insects, birds, cetaceans, vampire bats and primates (for reviews, see Feistner and McGrew, 1989; Stevens and Gilby, 2004). In the literature, food sharing is defined in many different ways and various theoretical models have been developed to consider the different biological situations where food sharing among animals occurs. In the rest of this chapter, we consider food sharing in kleptoparasitic populations, populations where foraging animals steal food discovered by others (see Section 1.6). We define food sharing to be the situation where the resource owner shows tolerance and allows a competitor animal to consume a part of its food although it has the ability to fight and try to keep all of its food. There are many game-theoretical models which investigate food sharing behaviour as an alternative strategy of foraging animals in aggressive populations. The Dove strategy in the famous and widely used Hawk–Dove game (Maynard Smith and Price, 1973; Maynard Smith, 1982, see also Section 1.3.1) can be thought of as an example of this non-aggressive behaviour. However, the Hawk–Dove game and a large number of variations of this game (see for example, Sirot, 2000; Dubois *et al.*, 2003) are unable to show why in many biological situations animals prefer to share the acquired prey avoiding any contests. The non-aggressive behaviour of the Dove is shown to never be a pure ESS, and can only exist as a mixed ESS (with Hawks) in a proportion depending on the value of the resource and the cost of a potential contest. This is mainly due to the fact that the Hawk–Dove game considers just a single contest between two strategies, the Hawk and the Dove strategy. Although the reward for adopting the Hawk strategy against an animal playing Hawk might be equal to or lower than the reward for adopting the Dove strategy, in a contest between a Hawk and a Dove, Hawk always receives the greater reward. However, in group foraging populations, animals usually have repeated interactions over food items. In iterated Hawk–Dove type games, it has been shown that if the attacked animal can adopt the strategy of its opponent (for example, play a Retaliator type strategy (Maynard Smith and Price, 1973; Maynard Smith, 1982) or a tit-for-tat type strategy (Axelrod and Hamilton, 1981)), then, under some circumstances, food sharing without any aggressive interactions might be an ESS (Dubois and Giraldeau, 2003, 2007). A different game-theoretical food sharing model is considered in Stevens and Stephens (2002) in a situation where the owner of the food might decide to share its food with a beggar due to the fitness costs of harassment or interference (e.g., screams, slapping of the ground, grabbing at the food). In this case, it is shown that food sharing might be the optimal choice for the food owner in situations where the fitness cost caused by the beggar's harassment, if the food is defended, exceeds the fitness cost of sharing.

In this chapter, we extend the model of kleptoparasitism presented in Broom *et al*. (2004) (see also Section 1.6) by assuming divisible food items and allowing animals to share their prey with attacking foraging animals. A foraging animal, encountering an animal handling a food item has the possibility to either attack attempting to steal or share the food, or just ignore it and continue foraging. On the other hand, an attacked animal which owns a food item, has the possibility to defend its food, to share it or to retreat leaving all the food to the attacking animal. Through a game-theoretical approach we examine the optimal strategy for an animal under different ecological circumstances.

6.2 The model

In a population of foragers of density P, each animal might either be in the state of searching for food, or the state where it is handling a food item that it has acquired. Let S denote the density of searchers and H the density of handlers. Each handler consumes the food item and resumes searching in a time drawn from an exponential distribution with mean t_h, so equivalently following a Markov process at rate t_h^{-1}.

Searchers are assumed to find food at rate $\nu_f f$. As well as finding food themselves when foraging, searchers can acquire food by trying to steal it from a handler, and they can search an area ν_h per unit time for handlers. Once a searcher comes upon a handler, it attacks to either steal or share the food item with probability p_1 or ignores the handler with probability $1 - p_1$ and continues searching for food. If the searcher attacks, the handler might decide to resist and defend its food item. This happens with probability p_3. In this case, the attacking searcher and the defender engage in a fight. Let A and R denote the density of attacking searchers and defenders, respectively. The rate at which searchers encounter handlers and engage in a fight (become attackers, A) is equal to $p_1 p_3 \nu_h H$, whereas handlers are found by searchers and resist a possible attack (become defenders, R) with rate $p_1 p_3 \nu_h S$. The fight lasts for a time drawn from an exponential distribution with mean $t_a/2$. The attacker animal wins the fight and becomes a handler with probability α and thus, with the same probability, the defender loses its food and starts searching again; so this happens at rate $2\alpha/t_a$. Otherwise, the attacking searcher loses the fight and returns to the searching state with rate $2(1-\alpha)/t_a$ and thus, with the same rate, the defender wins and continues handling its food. Note that the winner of the fight might face other subsequent challenges.

So far, the model described is the same as the model investigated in Broom *et al.* (2004). In this chapter, this model is extended by assuming that attacked animals can share a food item as follows. Assume that food items are divisible. The attacked handler might decide to share its food with an attacking searcher, with probability p_2. In this case, searchers become sharers with rate $p_1 p_2 \nu_h H$ and the attacked handlers with rate $p_1 p_2 \nu_h S$. Let C be the density of sharers. If the handler decides to share its food with the searcher, both take a half of the food. It is assumed, for reasons of simplicity, that both of the two sharers hold the food item and feed simultaneously on it. This discourages other animals from attempting to steal or share the food because this would be a difficult, risky and dangerous venture. So, food sharing results in the mutual protection of the two sharers from other predators. As a result, a sharer animal consumes its portion of the food item without any interruptions. Sharers eat their food unperturbed in a time drawn from an exponential distribution with mean t_c, or equivalently with rate t_c^{-1}. Once the halves of the food item have been consumed, the sharers start foraging again. Throughout this chapter, it is assumed that $2t_c \geq t_h$, that is, the decision of food sharing might either have no time cost or has some cost, but is never beneficial with respect to the handling time. The attacked handler, in order to avoid any time cost either from a fight or from the sharing process, might decide neither to defend its food item nor to share it, but to leave it to the attacking

Table 6.1: Notation of the game-theoretical model of food sharing in kleptoparasitic populations

Population's densities	**Meaning**
P	Density of the population
S, H, C, A, R	Density of searchers, handlers, sharers, attackers and defenders
Model Parameters	**Meaning**
$\nu_f f$	Rate at which foragers find undiscovered food
$\nu_h H$	Rate at which foragers encounter handlers
t_h	Expected time for a handler to consume a food item if it is not attacked
t_c	Expected time for a sharer to consume the half of a food item
$t_a/2$	Expected duration of a fight
α	The probability that the attacker wins the fight
Strategies	**Meaning**
p_1	The probability that a searcher attacks a handler when they meet
p_2	The probability that an attacked handler shares its food item
p_3	The probability that an attacked handler defends its food item

animal and return to the searching state. This happens with probability $1 - p_2 - p_3$ for any challenge, and so occurs at rate $p_1(1 - p_2 - p_3)\nu_h H$ for each searcher and rate $p_1(1 - p_2 - p_3)\nu_h S$ for each handler.

It should be noted that in the case where all the members of the population do not challenge, the strategy used by an animal in the handling position may be thought irrelevant because none of the animals will ever be attacked and thus each searcher finds a food item for itself in an average time equal to $1/\nu_f f$ and each handler consumes a discovered food item in time t_h. However, we assume that occasionally a challenge occurs "by mistake" (this is a version of the classical trembling hand argument of Selten (1975)). Thus, a handler animal of a population where animals never challenge, at some point might be faced by a foraging animal which attempts to steal or share the food.

The model parameters and notation are summarised in Table 6.1.

The differential equation based compartmental model that describes the dynamics of the different groups of the population in the above situation is the following

$$\frac{dS}{dt} = \frac{1}{t_h}H + \frac{1}{t_c}C + \frac{2}{t_a}(1-\alpha)A + \frac{2}{t_a}\alpha R - \nu_f fS - p_1(p_2+p_3)\nu_h SH, \tag{6.1}$$

$$\frac{dH}{dt} = \nu_f fS + \frac{2}{t_a}\alpha A + \frac{2}{t_a}(1-\alpha)R - \frac{1}{t_h}H - p_1(p_2+p_3)\nu_h SH, \tag{6.2}$$

$$\frac{dC}{dt} = 2p_1p_2\nu_h SH - \frac{1}{t_c}C, \tag{6.3}$$

$$\frac{dA}{dt} = p_1p_3\nu_h SH - \frac{2}{t_a}A, \tag{6.4}$$

$$\frac{dR}{dt} = p_1p_3\nu_h SH - \frac{2}{t_a}R. \tag{6.5}$$

The above system of equations is a closed system where the population density, P, remains constant, i.e.

$$P = S + H + C + A + R, \tag{6.6}$$

and one of the equations (6.1)–(6.5) is thus redundant. Note that because only two animals can be involved in a fight over a specific food item, the density of the attacking animals, A, is always equal to that of the attacked animals, R. Hence, mathematically, the variables A and R could be defined as one variable, for example $F = A + R$, and therefore the system of equations (6.1)–(6.5) could be reduced to four equations. However, because the attacking and the attacked animals might have different competitive abilities $(\alpha \neq 0.5)$, we distinguish the two classes. This distinction is useful in subsequent calculations when we consider the average time to the consumption of a food item, since when $\alpha \neq 0.5$, the time needed for the animals in each of the two classes is different (see Section 6.3).

We assume that the population rapidly converges to the equilibrium state (for a proof of this assumption for the original model of Broom and Ruxton (1998), see Luther and Broom (2004)). In the equilibrium conditions,

$$\frac{dS}{dt} = \frac{dH}{dt} = \frac{dC}{dt} = \frac{dA}{dt} = \frac{dR}{dt} = 0. \tag{6.7}$$

From the equation

$$\frac{dC}{dt} = 2p_1p_2\nu_h SH - \frac{1}{t_c}C = 0, \tag{6.8}$$

it follows that in the equilibrium, the number of sharers is given by

$$C = 2p_1p_2t_c\nu_h SH. \tag{6.9}$$

Similarly, from the equations

$$\frac{dA}{dt} = \frac{dR}{dt} = 0, \tag{6.10}$$

it is derived that the number of attackers and defenders in the equilibrium is given by

$$A = R = \frac{p_1 p_3 t_a \nu_h S H}{2}. \tag{6.11}$$

Substituting equations (6.9) and (6.11) into the system of equations

$$\frac{dS}{dt} = \frac{dH}{dt} = 0, \tag{6.12}$$

and solving the system for S using equation (6.6), it is obtained that in the equilibrium, the densities of the different groups of the population, S, H, C, A and R, are given by

$$(S,H,C,A,R) = \left(\frac{H}{t_h d(H,p_1,p_2)}, H, \frac{2p_1p_2t_c\nu_hH^2}{t_hd(H,p_1,p_2)}, \frac{1}{2}\frac{p_1p_3t_a\nu_hH^2}{t_hd(H,p_1,p_2)}, \frac{1}{2}\frac{p_1p_3t_a\nu_hH^2}{t_hd(H,p_1,p_2)}\right), \tag{6.13}$$

where $d(H, p_1, p_2) = \nu_f f - p_1 p_2 \nu_h H$, i.e. the difference between the rate at which searchers discover food items and the rate at which they become sharers. Note that this term is clearly positive since every food item can be shared at most once (and some are not shared) and it must be discovered beforehand. By (6.6) and (6.13), H is given by the biologically relevant solution of the quadratic equation

$$p_1\big(p_2(2t_c - t_h) + p_3t_a\big)\nu_hH^2 + \big(p_1p_2t_h\nu_hP + t_h\nu_f f + 1\big)H - t_h\nu_f fP = 0, \tag{6.14}$$

i.e. the positive solution,

$$H = \frac{-\big(p_1p_2t_h\nu_hP+t_h\nu_f f+1\big)+\sqrt{\big(p_1p_2t_h\nu_hP+t_h\nu_f f+1\big)^2+4p_1t_h\nu_f f\nu_hP\Big(p_2(2t_c-t_h)+p_3t_a\Big)}}{2p_1\nu_h\Big(p_2(2t_c-t_h)+p_3t_a\Big)}, \tag{6.15}$$

given that $2p_1\nu_h\big(p_2(2t_c - t_h) + p_3t_a\big) > 0$.

6.3 Optimal strategies

We are interested in finding conditions under which animals playing strategy (p_1, p_2, p_3), i.e. animals that attack handlers with probability p_1 and share or defend their food when they are attacked with probability p_2 and p_3, respectively, have greater fitness than animals playing any other strategy (q_1, q_2, q_3). We are ultimately looking for conditions when the overall strategy (p_1, p_2, p_3) is an ESS.

A strategy is considered to be optimal if it minimises the average time needed to the consumption of a food item. This minimisation results in the maximising of the long-term food intake rate of an animal playing this strategy and thus its fitness.

6.3.1 Average time for a single animal to consume a food item

Assume that a mutant animal playing strategy (q_1, q_2, q_3) invades into a population playing strategy (p_1, p_2, p_3).

If the mutant is in the searching state and encounters a handler it has two options:

- It attacks in order to share or steal the food item with probability q_1. Note that once it attacks, what will happen next depends on the handler' s strategy.
- It ignores the handler animal and continues searching for a food item for itself with probability $1 - q_1$.

If the mutant is in the handling state and is attacked by a searcher animal playing the population strategy it has three options:

- It shares the food item with probability q_2.
- It defends its food and a fight takes place with probability q_3.
- It leaves the food to the attacker and resumes searching with probability $1 - q_2 - q_3$.

Assume that a mutant searcher playing (q_1, q_2, q_3) has just come upon a handler playing the population strategy, (p_1, p_2, p_3). If the mutant searcher ignores the handler, with probability $1 - q_1$, then it will need an average time T_{S}^* until the consumption of a food item. Otherwise, if the mutant attacks, with probability q_1, the average time needed for the consumption of a food item depends on the action that the handler animal will take. If the handler decides to share the food, with probability p_2, then the further expected time required to the consumption of a whole food item by the mutant is T_{C}^*. If the attacked handler decides to defend its food, with probability p_3, then a fight takes place and the attacking mutant will need an average time T_{A}^* to consume a food item. Finally, if the attacked animal decides to leave its food to the attacking animal without taking any action, with probability $1 - p_2 - p_3$, the attacking searcher animal becomes a handler and it then requires an average time T_{H}^* until the consumption of a food item. T_{SA}^* is given by the following equation

$$T_{\mathrm{SA}}^* = q_1\big(p_2 T_{\mathrm{C}}^* + p_3 T_{\mathrm{A}}^* + (1 - p_2 - p_3) T_{\mathrm{H}}^*\big) + (1 - q_1) T_{\mathrm{S}}^*. \tag{6.16}$$

Table 6.2: Notation of the required times to the consumption of a food item from the different foraging states

Notation	Meaning
T_{SA}	The average time needed for a searcher animal who has just encountered a handler to consume a food item
T_{HA}	The average time needed for a handler animal who has just encountered a searcher to consume a food item
T_{S}	The average time needed for an animal who has just become a searcher to consume a food item
T_{H}	The average time needed for an animal who has just become a handler to consume a food item
T_{A}	The average time needed for an attacker who has just engaged in a fight to consume a food item
T_{R}	The average time needed for a defender who has just engaged in a fight to consume a food item
T_{C}	The average time needed for a sharer to consume a food item

Recall that we assume that two animals that share a food item do so equally. Each of the sharers needs a time t_c until consumption of the half of the food and once it consumes it, it returns to the searching state. From the searching state, the mutant needs a time on average equal to T_{S}^* in order to consume a whole food item. The average time needed for a mutant sharer to consume a whole food item, T_{C}^*, is given by

$$T_{\mathrm{C}}^* = t_c + \frac{T_{\mathrm{S}}^*}{2}. \tag{6.17}$$

The sharing process described above is, in terms of expected reward, entirely equivalent to a process where if a searcher and a handler decide to share the food, at the end of the sharing period, with probability 0.5 one of the two animals obtains the food item while the other takes nothing. The loser then has to resume searching for a new food resource and thus spend an average time T_{S}^* until the consumption of a food item. Both animals suffer a time cost from the sharing process equal to t_c. Hence, the time that a sharer needs for the consumption of a food item is on average equal to $0.5t_c + 0.5(t_c + T_{\mathrm{S}}^*)$, which leads to (6.17).
Substituting (6.17) into (6.16) we obtain

$$T_{\mathrm{SA}}^* = q_1\left(p_2 t_c + p_3 T_{\mathrm{A}}^* + (1 - p_2 - p_3)T_{\mathrm{H}}^*\right) + \left(1 - q_1 + \frac{q_1 p_2}{2}\right) T_{\mathrm{S}}^*. \tag{6.18}$$

An attacker animal that has just been involved in a fight will have a cost of an average time $t_a/2$ spent in the contest. With probability $1-\alpha$ the attacker loses the fight

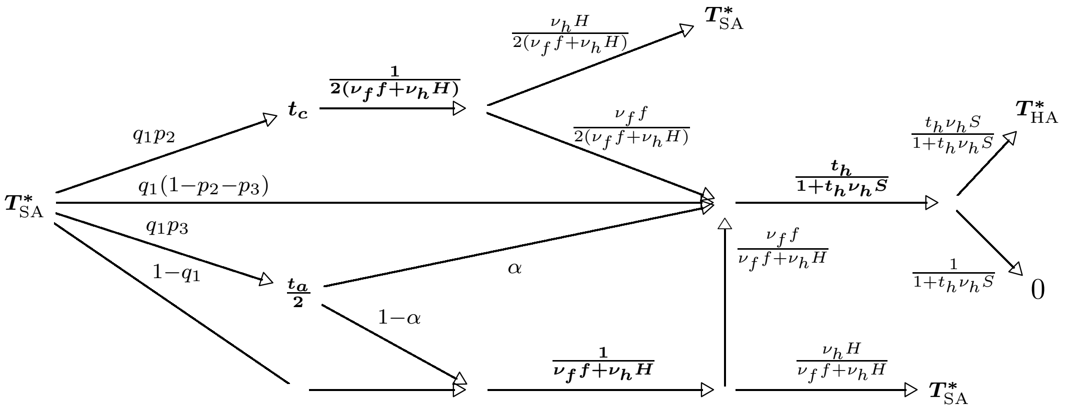


Figure 6.1: Schematic representation of all the possible events that might happen until the consumption of a food item by a mutant searcher playing strategy (q_1,q_2,q_3) who encounters a handler of a population playing strategy (p_1,p_2,p_3). The transition probabilities and the expected times (in bold) to move from one state to another are shown.

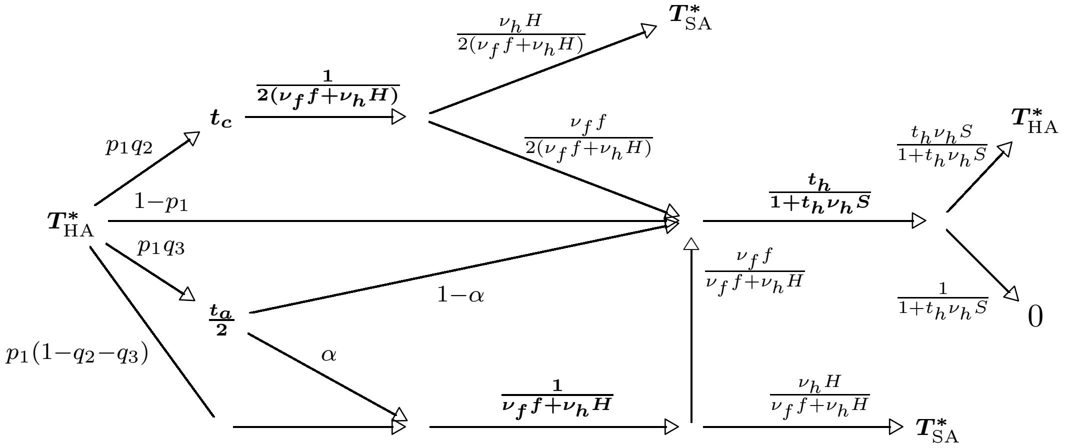


Figure 6.2: Schematic representation of all the possible events that might happen until the consumption of a food item by a mutant handler playing strategy (q_1,q_2,q_3) who encounters a searcher of a population playing strategy (p_1,p_2,p_3). The transition probabilities and the expected times (in bold) to move from one state to another are shown.

and starts searching again for food, whereas with a complementary probability α, it beats the defender and acquires the food item. Thus, T^*_{A} is given by the following equation

$$T^*_{\mathrm{A}} = \frac{t_a}{2} + (1-\alpha)T^*_{\mathrm{S}} + \alpha T^*_{\mathrm{H}}. \tag{6.19}$$

A searcher animal is looking either for a food resource or for a handler animal. At this stage, it spends an average time equal to $1\big/\big(\nu_f f + \nu_h H\big)$ before it finds either an unattended food item (this happens with probability $\nu_f f\big/\big(\nu_f f + \nu_h H\big)$) and becomes a handler, or a handler animal (with probability $\nu_h H\big/\big(\nu_f f + \nu_h H\big)$).

Thus, $T_{\rm S}^*$ is given by the following equation

$$T_{\rm S}^* = \frac{\nu_h H}{\nu_f f + \nu_h H} T_{\rm SA}^* + \frac{\nu_f f}{\nu_f f + \nu_h H} T_{\rm H}^* + \frac{1}{\nu_f f + \nu_h H}. \tag{6.20}$$

Once the searcher animal acquires a food item, it either consumes it without being found by any searcher animal, with probability $(1/t_h)\big/((1/t_h)+\nu_h S)$, or it is discovered by a searcher, with probability $\nu_h S\big/((1/t_h)+\nu_h S)$, resulting in an additional expected time cost $T_{\rm HA}^*$ until the consumption of a food item. The average time that the animal spends in the handling state before it either consumes its food item or is discovered by a searcher animal is equal to $1\big/((1/t_h)+\nu_h S)$. $T_{\rm H}^*$ is thus given by

$$T_{\rm H}^* = \frac{1}{1+t_h\nu_h S} 0 + \frac{t_h\nu_h S}{1+t_h\nu_h S} T_{\rm HA}^* + \frac{t_h}{1+t_h\nu_h S}. \tag{6.21}$$

The time needed for the mutant searcher, who has just come upon a handler playing the population strategy, to consume a food item, $T_{\rm SA}^*$, in the different scenarios is represented schematically in the diagram shown in Figure 6.1. The notation of food consumption times from the different foraging states is shown in Table 6.2.

Substituting equations (6.19), (6.20) and (6.21) into (6.18), after some calculations we obtain the following equation

$$\begin{aligned}
&\left(1-\left(1-q_1+\frac{q_1p_2}{2}+(1-\alpha)q_1p_3\right)\frac{\nu_h H}{\nu_f f+\nu_h H}\right)T_{\rm SA}^* = q_1p_2t_c + q_1p_3\frac{t_a}{2}+\\
&+\left(1-q_1+\frac{q_1p_2}{2}+(1-\alpha)q_1p_3\right)\frac{1}{\nu_f f+\nu_h H}+\\
&+\left(\left(1-\frac{q_1p_2}{2}\right)\nu_f f + q_1\big(1-p_2-(1-\alpha)p_3\big)\nu_h H\right)\frac{t_h(1+\nu_h S T_{\rm HA}^*)}{(1+t_h\nu_h S)(\nu_f f+\nu_h H)}.
\end{aligned} \tag{6.22}$$

If a mutant animal in the handling state is attacked by a searcher animal playing the population strategy, with a non-zero probability ($p_1 \neq 0$), then $T_{\rm HA}^*$ is given by the following equation

$$T_{\rm HA}^* = p_1\big(q_2T_{\rm C}^* + q_3T_{\rm R}^* + (1-q_2-q_3)T_{\rm S}^*\big) + (1-p_1)T_{\rm H}^*, \tag{6.23}$$

where $T_{\rm R}^*$ is the average time required until the consumption of a food item for a handler which decides to defend its food against a challenge. Substituting (6.17) into (6.23) we obtain

$$T_{\rm HA}^* = p_1\left(q_2t_c + q_3T_{\rm R}^* + \left(1-\frac{q_2}{2}-q_3\right)T_{\rm S}^*\right) + (1-p_1)T_{\rm H}^*. \tag{6.24}$$

In a similar way as before, T_{R}^{*} is given by

$$T_{\mathrm{R}}^{*} = \frac{t_a}{2} + \alpha T_{\mathrm{S}}^{*} + (1-\alpha) T_{\mathrm{H}}^{*}. \tag{6.25}$$

The time required for the attacked mutant handler to consume a food item, T_{HA}^{*}, in the different scenarios is represented schematically in the diagram shown in Figure 6.2.

Substituting equations (6.20), (6.21) and (6.25) into (6.24), we obtain

$$\begin{aligned}
&\left(1 - \frac{\left(\left(1-\frac{p_1 q_2}{2}\right)\nu_f f + \left(1 - p_1 + (1-\alpha) p_1 q_3\right)\nu_h H\right) t_h \nu_h S}{(1+t_h \nu_h S)(\nu_f f + \nu_h H)}\right) T_{\mathrm{HA}}^{*} = p_1 q_2 t_c + \\
&+ p_1 q_3 \frac{ta}{2} + p_1 \left(1 - \frac{q_2}{2} - (1-\alpha) q_3\right) \frac{1 + \nu_h H T_{\mathrm{SA}}^{*}}{\nu_f f + \nu_h H} + \\
&+ \left(\left(1 - \frac{p_1 q_2}{2}\right)\nu_f f + \left(1 - p_1 + (1-\alpha) p_1 q_3\right)\nu_h H\right) \frac{t_h}{(1+t_h \nu_h S)(\nu_f f + \nu_h H)}.
\end{aligned} \tag{6.26}$$

T_{SA}^{*} and T_{HA}^{*} are given by the solution of the system of equations (6.22) and (6.26). The average time required to the consumption of a food item for a single searcher animal who has just met a handler in a population where all animals play strategy (p_1, p_2, p_3), T_{SA}, and the respective time of a single handler of the same population who has just met a searcher, T_{HA}, can be found by solving the system of equations (6.22) and (6.26) substituting (p_1, p_2, p_3) for (q_1, q_2, q_3).

In the case where none of the animals of the population challenges any other animal, i.e. $p_1 = q_1 = 0$, but occasionally a challenge might occur "by mistake", the average time needed for the attacked handler animal to consume a food item if it adopts a strategy different from that of the population, $(0, q_2, q_3)$, is given by

$$T_{\mathrm{HA}}^{*} = q_2 \left(t_c + \frac{T_{\mathrm{S}}^{*}}{2}\right) + q_3 T_{\mathrm{R}}^{*} + (1 - q_2 - q_3) T_{\mathrm{S}}^{*}, \tag{6.27}$$

where T_{R}^{*} is given by equation (6.25). Because the population is not making challenges, $T_{\mathrm{S}}^{*} = (1/\nu_f f) + t_h$ and $T_{\mathrm{H}}^{*} = t_h$. Substituting into equation (6.27), we obtain that the average time needed for the attacked handler animal to consume a food item if it adopts a different strategy from that of the population, $(0, q_2, q_3)$, is given by

$$T_{\mathrm{HA}}^{*} = q_2 \left(t_c - \frac{1}{2}\left(\frac{1}{\nu_f f} + t_h\right)\right) + q_3 \left(\frac{t_a}{2} - (1-\alpha)\frac{1}{\nu_f f}\right) + \frac{1}{\nu_f f} + t_h. \tag{6.28}$$

If a mutant animal can invade a population then its strategy (q_1, q_2, q_3) must be a better strategy than that of the population (p_1, p_2, p_3) at least at one of the two decision points, when a searcher and potentially making a challenge or when receiving a challenge as a handler. A mutant that follows a different strategy from that of the population at just one decision point and where the strategy that is followed is better than that of the population, can obviously invade. When considering whether a particular strategy is an ESS or not, it is sufficient to investigate invasion by mutants which differ in strategy at one of the two decision points only. This is because if a mutant that differs in strategy at both of the decision points can invade, it must have a superior strategy at at least one of the decision points, and so an animal that shares the same strategy as the mutant at this decision point, and the same strategy as the population at the other, could also invade.

A mutant that uses a strategy different from that of the population at just the searching state is able to invade if $T^*_{\mathrm{SA}} \leq T_{\mathrm{SA}}$, i.e. if the decision that it will make at the point when it will meet a handler, when searching for food, will lead to at least as small a time until the consumption of a food item. Similarly, a mutant that plays differently from the population just at the handling state is considered to be able to invade if the decision it will make in an encounter with a searcher, when handling a food item, will not lengthen the time to the consumption of a food item, i.e. if $T^*_{\mathrm{HA}} \leq T_{\mathrm{HA}}$. Note that it is possible that under certain parameters T^*_{SA} is independent of q_1 and all values $0 \leq q_1 \leq 1$ give identical times. Similarly, T^*_{HA} might be independent of q_2 and q_3. In these circumstances, in such asymmetric games, the population can still be invaded by genetic drift.

Appendix C.1 investigates the possible existence of mixed ESSs. In some cases it is proved that at least for non-generic parameter sets there is no mixed ESS. In other cases it is not proved but extensive numerical investigation yields results consistent with no mixed ESS. Our working assumption from these results is that there are no mixed ESSs. Thus, if the population plays a non-pure strategy (p_1, p_2, p_3), for an invading animal there will be a pure strategy that will do at least as well as playing the population strategy, and so (p_1, p_2, p_3) could not be an ESS because this pure strategy would invade the population. Hence, we need to consider only two strategies for a foraging animal (always or never attempt to steal or share the prey of the other animal when the opportunities arise) and three strategic choices for an attacked animal (always share the food, always defend the food, or always surrender it to the attacking animal) as the components of the potential optimal strategy in any given population. Therefore, there are six possible pure strategies that an animal can use and need to be considered:

- Strategy (0,0,0) (Dove, D): the animal never challenges handlers and always retreats leaving the food to a challenger.

- Strategy (0,1,0) (Non-Attacking Sharer, NAS): the animal never challenges handlers and always shares its food when it is challenged.
- Strategy (0,0,1) (Retaliator, R): the animal never challenges handlers but always resists when it is challenged.
- Strategy (1,0,0) (Marauder, M): the animal challenges handlers at every opportunity but always retreats leaving the food to a challenger.
- Strategy (1,1,0) (Attacking Sharer, AS): the animal challenges handlers at every opportunity and always shares the food when it is challenged.
- Strategy (1,0,1) (Hawk, H): the animal challenges handlers at every opportunity and always resists any challenges.

6.3.2 The optimal strategy for an animal in the searching state

Consider a population playing strategy (p_1, p_2, p_3) that is potentially invaded by a mutant animal playing a different strategy (q_1, q_2, q_3). For reasons explained in the previous section, in order to study whether the mutant can invade because it uses a better strategy at the searching state, we assume that the strategy which is used by all the animals when they are in the handling state is the same, i.e. $p_2 = q_2$ and $p_3 = q_3$. We consider the strategy used by a searcher animal of the population when coming across a handler, p_1, to be advantageous over a mutant strategy, q_1, (and thus the population cannot be invaded by the mutant) if the average time required for the searcher playing the population strategy to gain and consume a food item, T_{SA}, is less than that required for the mutant searcher, T^*_{SA}. Using the equations (6.22), (6.26) and (6.13)–(6.15) we find all the necessary conditions under which a mutant playing strategy $q_1 \in \{0, 1 : q_1 \neq p_1\}$ cannot invade a population playing strategy $p_1 \in \{0, 1 : p_1 \neq q_1\}$ for the cases where either $p_2 = q_2 = 0$ and $p_3 = q_3 = 1$, $p_2 = q_2 = 1$ and $p_3 = q_3 = 0$, or $p_2 = q_2 = 0$ and $p_3 = q_3 = 0$. These are summarised in Table 6.3 (conditions (C.3), (C.6), (C.9), (C.10), (C.13) and (C.16)).

6.3.3 The optimal strategy for an animal in the handling state

In the handling position, an animal can use three strategies when it is challenged. It shares the food with the challenger, it defends its food, or it retreats leaving the food to the attacking animal, and depending on the ecological conditions it obtains the

Table 6.3: Conditions under which a mutant playing strategy (q_1, q_2, q_3) cannot invade a population playing strategy (p_1, p_2, p_3)

		Mutant's strategy, (q_1,q_2,q_3)					
		(0,0,0)	(0,1,0)	(0,0,1)	(1,0,0)	(1,1,0)	(1,0,1)
Population's strategy, (p_1,p_2,p_3)	(0,0,0)	/	$2t_c - t_h > \frac{1}{\nu_f f}$ **(C.1)**	$\nu_f f > \frac{2(1-\alpha)}{t_a}$ **(C.2)**	The mutant always invades **(C.3)**	—	—
	(0,1,0)	$2t_c - t_h < \frac{1}{\nu_f f}$ **(C.4)**	/	$2t_c - t_h < t_a - \frac{1-2\alpha}{\nu_f f}$ **(C.5)**	—	$2t_c - t_h > \frac{1}{\nu_f f}$ **(C.6)**	—
	(0,0,1)	$\nu_f f < \frac{2(1-\alpha)}{t_a}$ **(C.7)**	$2t_c - t_h > t_a - \frac{1-2\alpha}{\nu_f f}$ **(C.8)**	/	—	—	$\nu_f f > \frac{2\alpha}{t_a}$ **(C.9)**
	(1,0,0)	The mutant never invades **(C.10)**	—	—	/	$2t_c - t_h > \frac{1}{\nu_f f}$ **(C.11)**	$\nu_f f > \frac{2(1-\alpha)}{t_a} - \frac{t_h \nu_f f \nu_h P}{t_h \nu_f f + 1}$ **(C.12)**
	(1,1,0)	—	$2t_c - t_h < \frac{1}{\nu_f f - \nu_h H_a}$ * **(C.13)**	—	$2t_c - t_h < \frac{1}{\nu_f f - \nu_h H_a}$ * **(C.14)**	/	$(2t_c - t_h)(\nu_f f - \alpha \nu_h H_a)\nu_f f <$ $(t_a \nu_f f + \alpha)\nu_f f + (1-\alpha)\big((t_h \nu_h P -$ $1)\nu_f f - (\nu_f f + \nu_h P) t_h \nu_h H_a\big)$ * **(C.15)**
	(1,0,1)	—	—	$\nu_f f < \frac{2\alpha}{t_a}$ **(C.16)**	$\nu_f f < \frac{2(1-\alpha)}{t_a} + (1-2\alpha)\nu_h H_b$ ** **(C.17)**	$(2t_c - t_h)(\nu_f f + \alpha \nu_h H_b) >$ $t_a(\nu_f f + 2\alpha \nu_h H_b) +$ $\alpha t_h \nu_h (P - H_b) + 2\alpha - 1$ ** **(C.18)**	/

$^{*}H_a$ is given by the solution of the equation $(2t_c - t_h)\nu_h H_a^2 + (t_h \nu_f f + t_h \nu_h P + 1)H_a - t_h \nu_f f P = 0$.

$^{**}H_b$ is given by the solution of the equation $t_a \nu_h H_b^2 + (t_h \nu_f f + 1)H_b - t_h \nu_f f P = 0$.

highest benefit when it always takes one of these three actions. As before, assume that a population already at equilibrium conditions is invaded by a mutant, which now uses a different strategy as a handler but the same strategy as a searcher.

Optimal strategies in an aggressive population

Assume that all the members of the population behave aggressively when encountering a handler animal, i.e. $p_1 = q_1 = 1$. We consider the strategy of an attacked handler of the population to be advantageous over the strategy used by an attacked handler mutant (and thus the mutant cannot invade) if the average time required for the first to consume a food item, T_{HA}, is less than that required for the second, T^*_{HA} (in this case, this is equivalent to the comparison of T_{SA} with T^*_{SA} because the times needed for animals which always challenge, i.e. when $p_1 = q_1 = 1$, to acquire a food item and be discovered by a foraging animal are identical, independently of the strategies they use as handlers). Using again equations (6.22), (6.26) and (6.13)–(6.15) we find the necessary conditions under which a mutant in this scenario cannot invade a population playing a different strategy at the handling state. These conditions are presented in Table 6.3 (conditions (C.11), (C.12), (C.14), (C.15), (C.17) and (C.18)).

Optimal strategies in a non-aggressive population

In the case where all the members of the population do not challenge, i.e. $p_1 = q_1 = 0$, an animal of the population playing $(0, p_2, p_3)$ does better than a mutant playing $(0, q_2, q_3)$, and thus the population cannot be invaded by this mutant, if $T_{\mathrm{HA}} < T^*_{\mathrm{HA}}$, where by (6.28) ($T_{\mathrm{HA}}$ in this case is similarly given by (6.28) substituting p_2 and p_3 for q_2 and q_3, respectively) we obtain the condition

$$(q_2 - p_2)\left(t_c - \frac{1}{2}\left(\frac{1}{\nu_f f} + t_h\right)\right) + (q_3 - p_3)\left(\frac{t_a}{2} - (1-\alpha)\frac{1}{\nu_f f}\right) > 0. \qquad (6.29)$$

The conditions under which a mutant playing strategy $(0, q_2, q_3)$ is unable to invade a population playing strategy $(0, p_2, p_3)$ are summarised in Table 6.3 (conditions (C.1), (C.2), (C.4), (C.5), (C.7) and (C.8)).

6.4 Evolutionarily Stable Strategies

Table 6.3 shows all the appropriate conditions under which a population playing strategy (p_1, p_2, p_3) cannot be invaded by a mutant playing a different strategy at one

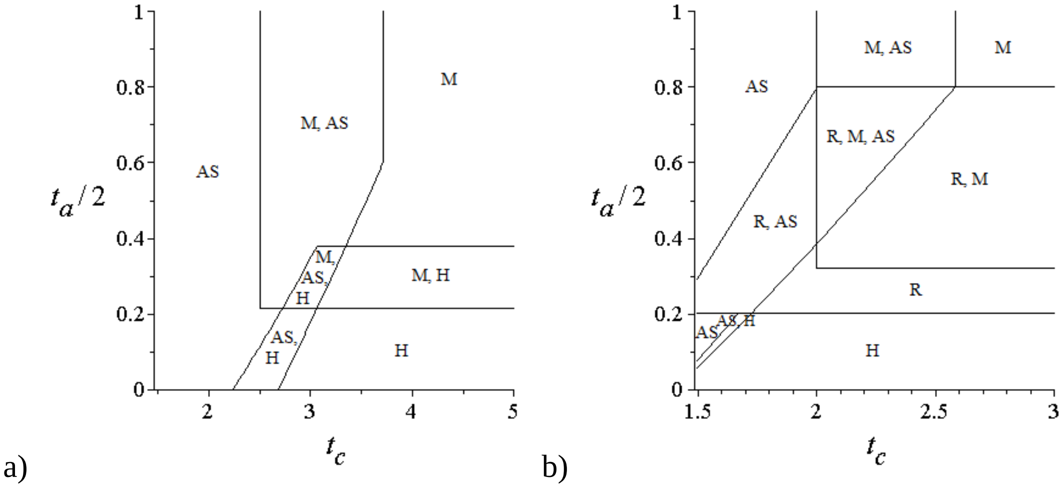


Figure 6.3: Graphs showing examples of the region where each of the four possible ESSs (Retaliator (R), Marauder (M), Attacking Sharer (AS) and Hawk (H)) is an ESS as the duration of the content, $t_a/2$, and the handling time of a sharer, t_c, vary. In each region, a single letter 'X' indicates that the strategy X is the unique ESS, 'X,Y' indicates that the strategies X and Y are simultaneous ESSs, and 'X, Y, Z' that the three strategies X, Y and Z are simultaneous ESSs. (a) $t_h = 3, \nu_f f = 0.5, \nu_h = 1.5, \alpha = 0.7, P = 1$, (b) $t_h = 3, \nu_f f = 1, \nu_h = 2, \alpha = 0.2, P = 1$.

of the two decision points, (q_1, q_2, q_3), for all the possible cases where all animals play a pure strategy.

According to the results shown in Table 6.3, strategies (0,0,0) and (0,1,0) can never resist all of the possible invading strategies and there are thus four possible ESSs:

- Strategy (0,0,1) is an ESS if the conditions (C.7), (C.8) and (C.9) are satisfied.
- Strategy (1,0,0) is an ESS if the conditions (C.11) and (C.12) are satisfied.
- Strategy (1,1,0) is an ESS if the conditions (C.13), (C.14) and (C.15) are satisfied.
- Strategy (1,0,1) is an ESS if the conditions (C.16), (C.17) and (C.18) are satisfied.

Figure 6.3 shows the regions in parameter space in which each of the four strategies, Retaliator, Marauder, Attacking Sharer and Hawk, is an ESS, for specific parameter values as the duration of the contest, $t_a/2$, and the handling time of a sharer, t_c, vary. Figure 6.4 shows how these regions vary as the density of the population, P, and the rate at which foragers find undiscovered food, $\nu_f f$, vary.

Obviously, these regions in the $t_a/2 - t_c$ plane in Figure 6.3 and $P - \nu_f f$ plane in Figure 6.4 will vary, depending on the other parameter values. However, some

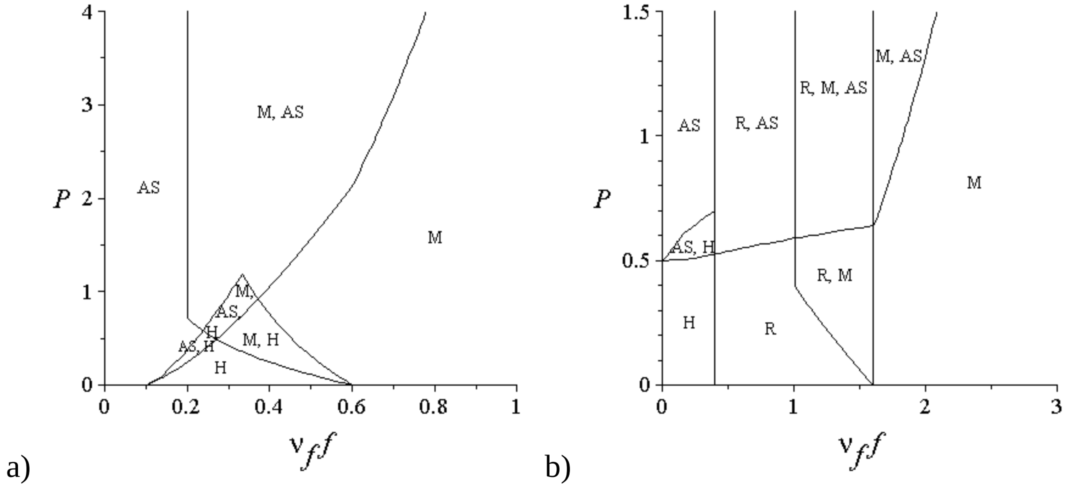


Figure 6.4: Graphs showing examples of the region where each of the four possible ESSs (Retaliator (R), Marauder (M), Attacking Sharer (AS) and Hawk (H)) is an ESS as the density of the population, P, and the rate at which foragers find undiscovered food, $\nu_f f$, vary. In each region, a single letter ‘X’ indicates that the strategy X is the unique ESS, ‘X,Y’ indicates that the strategies X and Y are simultaneous ESSs, and ‘X, Y, Z’ that the three strategies X, Y and Z are simultaneous ESSs. (a) $t_a/2 = 0.5, t_h = 3, t_c = 4, \nu_h = 1.5, \alpha = 0.7$, (b) $t_a/2 = 0.5, t_h = 3, t_c = 2, \nu_h = 2, \alpha = 0.2$.

general conclusions can be extracted. Figure 6.3 and Figure 6.4 suggests that between the regions where two strategies are unique ESSs, there can be a region where the two strategies are simultaneous ESSs and among the regions of three pairs of ESSs configured by three strategies, there might be a region where the three strategies might coexist as ESSs. This excludes the possibility of the Retaliator and the Hawk strategies being simultaneous ESSs, because this can never happen due to the contradiction of the conditions (C.9) and (C.16) (see Table 6.3). This gives eleven distinct regions as summarised in Figure 6.3 and Figure 6.4. It appears that every set of parameters yields one or more pure ESSs. Numerical examples on a wide range of parameter values indicate that there is no parameter set where this is not the case i.e. that there are not any mixtures of strategies or cases where there are no ESSs. Although we do not believe that there will be any parameter set where there will be such a polymorphic mixture or no ESS (in similar models such cases do not occur, and for an argument that actual mixed ESSs are not possible, see Appendix C.1), we cannot definitively rule out this possibility.

6.5 Predictions of the model

In the case where neither the members of the population nor any mutant share the food, i.e. in the case where $p_2 = q_2 = 0$, all the above results agree with the results obtained in previous work (Broom *et al.*, 2004). Hence, here we concentrate on the cases where the members of the population or a mutant animal or both, always share their food when they are attacked, i.e. cases where either p_2 or q_2 or both are equal to 1. This provides both new potential ESSs and also new mutant strategies to invade other strategies, so that strategies that were ESSs in Broom *et al.* (2004) will no longer be in some cases.

In a non-attacking population, a sharer does better than a Dove when they are attacked if the average time needed for a sharer to consume a whole food item $(t_c + ((1/\nu_f f) + t_h)/2)$ is less than the average time needed to find an undiscovered food item $(1/\nu_f f)$ and consume it (t_h) (equivalently in this case, if the time the sharer needs to consume the half of the food item (t_c) is on average less than half of the time needed to find and consume a whole food item $(((1/\nu_f f) + t_h)/2)$). On the other hand, an Attacking Sharer mutant does better than a member of a population of Non-Attacking Sharers if $t_c \leq ((1/\nu_f f) + t_h)/2$ as well. Hence, as we see in Table 6.3, condition (C.4) contradicts condition (C.6) and thus a Non-Attacking Sharer is never an ESS. The food sharing strategy can be an ESS only if the sharer challenges a handler at every opportunity when it is in the searching state. A population of Attacking Sharers can potentially be invaded by Non-Attacking Sharers, Marauders and Hawks. The conditions under which a Non-Attacking Sharer and a Marauder can invade a population of Attacking Sharers are the same. This occurs because in such a population a Marauder can invade if it is better for any handler to give up a food item rather than share (so being a searcher is better than sharing a food item) and a Non-Attacking Sharer can invade if it is better not to challenge for a food item that will be shared (so again searching is better than sharing). Increasing the rate at which foragers find food, $\nu_f f$, increases the parameter range where Non-Attacking Sharers and Marauders invade the population of Attacking Sharers. Depending on the values of the other parameters, the increase of $\nu_f f$ might favour the invasion of Hawks as well (usually when food is difficult to discover). Hence, increasing $\nu_f f$ decreases the range of the parameter values in which the Attacking Sharer strategy is an ESS (see Figure 6.4 for an example). A similar situation appears by decreasing the area in which foragers search for handling sharers per unit time, ν_h. As is observed in the conditions (C.13)–(C.15) and Figure 6.4, the decrease of the density of the population, P, might also create unpropitious circumstances for food sharing. For a given set of parameter values for which the Attacking Sharer strategy is an ESS, increasing the time cost of the sharing process, which results in the increase of t_c, the area where the Attacking Sharer strategy is an ESS reduces, as one would expect. Depending on the other ecological conditions, this strategy might coexist as an ESS with either one of the other possible ESSs (Retaliator, Marauder or Hawk) or two of them (Retaliator and Marauder or Marauder and Hawk). At very high levels of t_c such that the time spent in sharing would be better spent in searching for another food item or in defending the food item, Attacking Sharer cannot be an ESS. In this case, the predictions of the model approach those of the model of Broom *et al*. (2004), where sharing was not possible (see Figure 6.3 for an example). In conditions where the duration of aggressive interactions is high, the defending strategy is less profitable and thus the avoidance of any aggressive interaction is favoured. Hence, under these circumstances, it is observed that animals should decide either to surrender their food (use the Marauder strategy) or to share it (use the Attacking Sharer strategy) when they are challenged, even if they have a high probability of defending their food successfully. Therefore, at high fight durations each of Marauder and Attacking Sharer strategies might be the unique ESS or both might be ESSs simultaneously (see Figure 6.3 for an example).

6.5.1 A special case

As a special case, we consider the case where $2t_c = t_h$, i.e. where sharing does not reduce the speed of food consumption. The results obtained in this case are shown in Table 6.4. It is observed that, as well as the Dove and Non-Attacking Sharer strategies, which as we have seen in the previous section are never ESSs, in this case the Marauder strategy is also never an ESS because it can always be invaded by an Attacking Sharer animal. The Attacking Sharer strategy can only be invaded by the Hawk strategy. Moreover, this can happen just in the few cases where the chance of a successful defence is relatively high, i.e. the probability α is relatively small, and the time spent in a contest, $t_a/2$, is small. For $\alpha \geq 0.5$, the conditions (C.7) and (C.9) indicate that the Retaliator strategy can never be an ESS. In this case, the condition (C.18) also indicates that an Attacking Sharer can always invade a population playing Hawk and thus the Hawk strategy can never be an ESS as well. Hence, at least for $\alpha \geq 0.5$, Attacking Sharer is the only ESS no matter what the other parameter values are. The Hawk strategy is an ESS mainly when $t_a/2$ and α are small. As $t_a/2$ and/or α increase, depending on the other parameter values, there might be a range where the pure Hawk ESS coexists with the pure Attacking Sharer ESS. When the defender is likely to succeed, i.e. α is small, defence of the food item might be the favoured strategy even if the fight time is relatively long, especially in cases where available food is scarce. Hence, there is a range where either pure Retaliator is the only ESS, or the pure Retaliator ESS coexists with the pure Attacking Sharer ESS. Although such ecological conditions favour a handler animal defending its food in

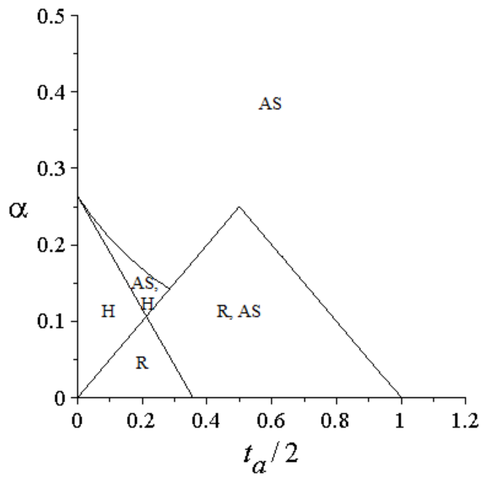


Figure 6.5: A graph showing an example of the region where each of the three possible ESSs (Retaliator (R), Attacking Sharer (AS) and Hawk (H)) can occur in the special case where $2t_c = t_h$, as the probability α of the challenger winning and the duration of the content, $t_a/2$, vary. In each region, a single letter 'X' indicates that the strategy X is the unique ESS, 'X,Y' indicates that the strategies X and Y are simultaneous ESSs, and 'X, Y, Z' that the three strategies X, Y and Z are simultaneous ESSs. $2t_c = t_h = 3, \nu_f f = 0.5, \nu_h = 1.5, P = 1$.

a fight, in an Attacking Sharer population the subsequent potential attacks that a defender faces make the defending strategy less attractive. For similar reasons, in a population that is using the Attacking Sharer ESS, every searcher should attempt to share. Now, in a population using the Retaliator ESS, defending the food is a more attractive strategy than sharing it because a successful defence is likely and animals in the population do not attack. On the other hand, attacking a handler and engaging in a fight in conditions where aggressive interactions favour the attacked handler is not a good strategy and thus attacking strategies cannot invade.

Figure 6.5 shows a region with all the possible ESSs in this specific case, as the probability α of the challenger winning and the duration of the content, $t_a/2$, vary.

6.6 Discussion

Food sharing is a very common tactic adopted by a broad group of animal species for their survival. Using a game-theoretical approach, the present model investigates the ecological circumstances under which animals should share their food when they are challenged by other foraging animals. We have extended the game-theoretical model of Broom *et al*. (2004) by allowing animals to share their food. Animals in the present model can choose among two additional strategies; either to attempt to share or steal the food from a handler when foraging and share their food when they are challenged by a forager, or to ignore any opportunities to share or steal the food

Table 6.4: Conditions under which a mutant playing strategy (q_1, q_2, q_3) cannot invade a population playing strategy (p_1, p_2, p_3) in the special case where $2t_c = t_h$

		Mutant's strategy, (q_1, q_2, q_3)					
		(0,0,0)	(0,1,0)	(0,0,1)	(1,0,0)	(1,1,0)	(1,0,1)
Population's strategy, (p_1, p_2, p_3)	(0,0,0)	/	The mutant always invades	$v_f f > \frac{2(1-\alpha)}{t_a}$	The mutant always invades	—	—
	(0,1,0)	The mutant never invades	/	$v_f f > \frac{1-2\alpha}{t_a}$	—	The mutant always invades	—
	(0,0,1)	$v_f f < \frac{2(1-\alpha)}{t_a}$	$v_f f < \frac{1-2\alpha}{t_a}$	/	—	—	$v_f f > \frac{2\alpha}{t_a}$
	(1,0,0)	The mutant never invades	—	—	/	The mutant always invades	$v_f f > \frac{2(1-\alpha)}{t_a} - \frac{t_h v_f f v_h P}{t_h v_f f + 1}$
	(1,1,0)	—	The mutant never invades	—	The mutant never invades	/	$(t_a v_f f + \alpha)(t_h v_f f + t_h v_h P + 1) - (1-\alpha)(t_h v_f f + 1) > 0$
	(1,0,1)	—	—	$v_f f < \frac{2\alpha}{t_a}$	$v_f f < \frac{2(1-\alpha)}{t_a} + (1-2\alpha) v_h H_b$ *	$t_a(v_f f + 2\alpha v_h H_b) + \alpha t_h v_h (P - H_b) + 2\alpha - 1 < 0$ *	/

[*] H_b is given by the solution of the equation $t_a v_h H_b^2 + (t_h v_f f + 1) H_b - t_h v_f f P = 0$.

of other animals when foraging but share when another animal attacks. This model is likely to be an improvement if caught food items are at least partly divisible, for instance fruit species (e.g., White, 1994), as opposed to for example a nut or a fish (e.g., Iyengar, 2008) that are hard to divide, in which case the original modelling system will be more appropriate. At the opposite extreme, in situations where food items come in patches, for instance seed patches (e.g., Barnard and Sibly, 1981), which are easily divisible, then the producer-scrounger type models (e.g., Dubois and Giraldeau, 2003; Dubois *et al*., 2003; Dubois and Giraldeau, 2005, 2007) could be appropriate models.

Considering the time needed for a food item to be acquired and consumed, the model predicts that there is a wide range of ecological conditions in which attempting to share or steal the food at every opportunity and sharing the food when attacked is the optimal strategy that should be used by animals. The non-aggressive strategy where animals do not challenge other animals but share their food when challenged can never be an ESS because, depending on the ecological parameters, this strategy is always invaded either by the Dove or by the Attacking Sharer strategy. This adds one possible ESS to the model of Broom *et al*. (2004). Investigation of the model suggests that under any ecological parameters, there is always at least one ESS that an animal can use. Every two ESSs can occur as ESSs simultaneously, apart from the Retaliator and the Hawk strategy where it is shown that they can never be ESSs simultaneously. It is also possible that under some conditions there are three simultaneous ESSs (Retaliator, Marauder and Attacking Sharer, or Marauder, Attacking Sharer and Hawk).

Different ecological factors might influence the strategic choice of food sharing. Food availability is one of the crucial factors. In conditions of limited food availability the use of the Attacking Sharer strategy is enhanced, whereas at high food densities food sharing becomes a less profitable strategy. A high time cost of food defence, a small probability of a successful food defence, a high rate at which searchers encounter handlers, a high population density and a low time cost of food sharing are also conditions which favour animals sharing their food. In the special case where food sharing has no additional time cost, foraging animals should almost always attempt to share food with a handler and handlers should almost always share their food. Defending the food might be the optimal strategy for the owner, especially when food is difficult to be discovered, and the success of this is likely. Moreover, attacking at every opportunity and defending when attacked is an ESS in limited cases, where the time cost of the defence is small, but never attacking and always defending might be an ESS even if the defence will result in a high time cost.

Attacking and always retreating when attacked never occurs in this case because sharing is always a better strategy.

Food sharing is a complicated mechanism. Different animal species share their food for different reasons and under different ecological and biological conditions. In many situations, food sharing is a voluntary process where animals choose to share their food without any kind of menace from other foraging animals. This process might result in immediate benefits for animals, for example the creation of cooperation for the increase of foraging success or predation avoidance, or the increase of mating opportunities (see Stevens and Gilby, 2004). It is also often the case that sharing occurs between relatives or between animals with a social interaction, even if those animals are not relatives, e.g. between roost mates (Wilkinson, 1990). In such cases, food sharing might not be immediately beneficial but result in long term benefits such as future reciprocal sharing, i.e. altruism (see Stevens and Gilby, 2004). In the present model, food sharing is considered to be the process where a food owner shows tolerance to an attacking foraging animal and shares its food with it, although it would be better for the owner not to be discovered by any other animal. This animal behaviour might occur, for example, in cases where a beggar challenges a food owner, a situation which is observed in monkeys and chimpanzees populations (for examples of this behaviour, see Stevens and Gilby (2004)). A particular feature of our model compared with other models in the literature, is that by sharing food, the two animals protect each other from potential subsequent costly challenges that might extend the time until the consumption of a food item. Hence, on average a half of the food item is consumed without the risk of other delays apart from the time required for sharing. This, under certain conditions, might be the least costly process with respect to the expected time needed for the consumption of food and thus a process which maximises the food intake rate. Although there is no empirical data to support precisely the above assumptions, there is evidence that in nature, animals in many cases prefer to share food with other animals to reduce the risk of losing the entire prey. For example, a lion instead of defending its prey against an approaching member of the pride, might share it in order to increase the efficiency of defending the prey from invading hyenas (see for example, Cooper, 1991; Stevens and Gilby, 2004).

In addition, our model assumes that the members of the population are of the same type. However, real populations consist of individuals with biological and physiological differences and the optimal strategic choices depend on the characteristics of the individuals and those of their opponent. For example, recent observational and experimental studies on the dung roller beetle *Canthon cyanellus*

cyanellus have shown that males of similar size are more likely to share the resource rather than to fight over this (Chamorro-Florescano *et al.*, 2011). Fight duration may be correlated with the differences between the opponents as well (e.g., Rovero *et al.*, 2000). The size and the quality of the food items or the estimation of the value of the resource might also affect significantly the frequency of food sharing (e.g., White, 1994) as well as the contest duration (e.g., Enquist and Leimar, 1987).

In our model all costs are expressed in terms of time used and we ignore other costs which can be important, such as energy costs and possible injuries resulting from fights (for a model which incorporates energy costs see Vahl, 2006). For simplicity, we also do not impose extra time penalties on animals in contests. A resulting limitation is that the winner and the loser of a contest face the same cost. Although this can be the case in nature (e.g., Smith and Taylor, 1993), experimental studies have shown that either the loser (e.g., Chellappa and Huntingford, 1989; Neat *et al.*, 1998) or the winner (e.g., Hack, 1997) might suffer higher energetic or other cost, such as a high recovery time cost. For instance, if the handler uses more energy (e.g., because it is carrying a food item during the contest) then it might need a higher recovery time. This would decrease the food intake rate making the defending strategy less attractive and the choice of alternative strategies more likely (see also, Luther and Broom, 2004). In the same way, although it is assumed that the cost from the sharing process is equal for the two animals that share food, in reality the two animals might suffer a different cost. Furthermore, it is assumed that once an animal loses a contest with another animal, it does not initiate a new fight with the same animal but starts searching for alternative food resources. This is generally reasonable, as often contests between animals can have strong (at least short-term) effects on their relationship (winner and loser effects) which reinforce the dominance of the winner (see for example, Dugatkin, 1997). Similarly, in related contests between animals for territory acquisition, animals that lose an agonistic interaction often leave the areas in which they were defeated (see for example, Stamps and Krishnan, 1994). However, we should note that in some cases an animal may attack repeatedly the owner after iterated losing tries (e.g., Stamps, 1994). One way that the model could be extended and relax this assumption is by introducing the choice to the loser animal to attack the winner again or not, following similar assumptions to those made in some owner-intruder types of games (e.g., Morrell and Kokko, 2003).

Another interesting extension of the model that could add some realism is to assume that the attacking animal, after its first attack, has the possibility to update its strategy based on the decision of the attacked handler. For example, it could be assumed that if the attacking searcher is offered a share, it has the possibility to either give up and resume searching for another food item, or attack again attempting to get the whole food item from the present handler. A handler sharer, being attacked again by the attacking searcher either defends the food and a fight takes place or it retreats and leaves the food to the attacker in order to avoid a fight. This extension would add new strategic choices for the animals. However, it would not add any new observable behaviour (at any time the new strategies will look exactly the same as the strategies in the model considered in this chapter). Although an analysis of such extended models is required in order to extract safe conclusions, we predict that the new strategies under some conditions might be able to invade other strategies that in the current model are ESSs. This would reduce the regions in parameter space where each of the current strategies is evolutionarily stable. For example, we can predict that under some circumstances, an animal should attack again a handler that offers a share in the first attack but will give up on a second attack. In the current model, for very large fight duration, $t_a/2$, the optimal strategy for an attacked handler might be to offer a share to an attacking searcher and the optimal strategy for the challenger to accept the share (see for example Figure 6.3). However, if the challenger has the possibility to attack again, then this would be the best strategic choice for it because the defender will retreat and leave the food item to the attacker rather than defend it and engage in a very long fight. Similarly, when $t_a/2$ is small, it might be optimal for an attacked handler to offer a share (see Figure 6.3). However, in the extended model, it might be better for the challenger to attack again because it will be worth fighting for the whole food item.

In natural systems, foraging animals might be faced with more than one foraging option with different variance in food intake. For example, they might be faced with a constant food resource versus a variable food resource, a food resource with fixed delay versus the same food resource with variable delay, or an immediate gain of food versus a delayed gain. There is strong empirical evidence that a forager's choice may depend on many ecological factors, such as the energetic status of the animal, the type of food variance, the energy requirements of the animal within a certain time interval and the probability of delays due to different kinds of unpredictable interruptions (for example bad weather). The forager might be either risk-averse and choose the predictable option, or risk-prone and choose a risky option, respectively (see for example, Kacelnik and Bateson, 1996). For example, an animal with low food reserves might choose a safe lower level of return, provided it is sufficient for survival. Food sharing might be a way for animals to reduce such variances in food intake (e.g., Wenzel and Pickering, 1991). Although the present model does not consider any risk associated with alternative food sources, it would be interesting to incorporate in future work such parameters that might influence the foraging decisions.

Further research taking into consideration all these different factors will help us to better understand the reasons why and the conditions under which animals prefer to share their food.

CHAPTER 7

Conclusions and future work

In this research work, considering the evolutionary process in structured populations, through either an analytic approach on some simple graph structures or the use of approximation and numerical methods on complex graph structures, it has been demonstrated that the dynamics of an evolving population might be significantly influenced by the structure of the population. In stochastic evolutionary dynamics, the population structure might remarkably enhance selection and eliminate random drift or vice versa. The extent of the structure effect depends on the update rules of the evolutionary dynamics, on the fitness of individuals as well as on the population size.

The significance of the consideration of the time required for the evolutionary process to end has also been highlighted. This quantity is usually ignored and an emphasis is given just to the probability of fixation. However, in some cases, the fixation probability is not sufficient to describe the evolution of the system, since a given type of individual might have a very high chance to fixate but this might need extremely long time to happen.

The possibilities for analytic investigations of the evolutionary dynamics in structured populations are very limited and numerical and approximation methods are essential for the exploration of the dynamics in complex structures. In this work, a powerful approximation method has been proposed. This method can effectively approximate the results of the evolutionary process in a broad class of structures and could give insight to the effect of the population structure on evolutionary dynamics.

In all evolutionary processes that have been considered in this work, it has been assumed that there is only a selection process and no mutation occurs during the process. The results derived can also be applied in processes where the mutation rate is very small, since in these cases the system will reach an absorbing state and stay there for a very long time before a new mutation occurs. The limit of zero or very small mutation rate is a basic assumption that has been made in most of the studies on evolutionary processes in graph structured populations. However, there are evolutionary processes with high mutation rates, especially genetic processes, such as the evolution of many populations of bacteria and viruses. It would be interesting to consider how mutation affects the evolutionary process in structured populations. Obviously, if in the processes considered in this work there is a high mutation rate (an individual playing strategy X can reproduce an individual playing Y, or vice versa, with high probability), evolution will drive the system away from the absorbing states and both strategies will always present in the population. In such cases, it would be interesting to study the stationary probability distribution of the system and find appropriate conditions under which the average abundance of strategy X is higher than the average abundance of strategy Y. Of course, the consideration of an evolutionary process with arbitrary mutation rates will be more complicated, even in simple graphs. In some cases, the number of states that the system can reach as well as the number of possible transitions will increase because it will be possible an individual of type X is replaced by an individual of type Y which is an offspring of a neighbouring individual of type X. For example, even on simple graphs like a circle, the number of the reachable possible states starting from any connected segment of mutant individuals would increase dramatically, since any connected segment could split into two. On a star graph, the state where all individuals but the centre one are of the same type would also be reachable (in the case of zero mutation rate, the system can reach such a state only if it starts from it at the beginning of the process). The approximation model presented in Chapter 4 could be extended for the study of evolutionary processes with arbitrary mutation rates in a large class of graphs.

A limitation of the evolutionary models in graph structured populations is that they consider pairwise interactions between neighbouring individuals, which are represented by the edges of the graph. However, in real populations many individuals might interact simultaneously. For example, more than two animals might fight over a food item, over territorial possession or other resource. Broom and Rychtář (2012) have proposed a new modelling framework for the study of evolutionary dynamics in structured populations. They introduced a model for the competition between territorial animals where animals can move between different territories with a certain probability and interact with other animals. The size of the interacting groups is varied, depending on the structure of the territories and the probabilities of the animals being in each territory. This model could be extended for the study of evolutionary game dynamics in such structured populations following some update rules. This would allow us to examine the effect of the population structure in more realistic scenarios. This modelling framework could also be applied for the modelling of kleptoparasitism in structured populations where animals in the different territories could have different rates of discovering a food item and encountering handlers.

In van Veelen and Nowak (2012), following the work of Gokhale and Traulsen (2010) and previous theoretical models in well-mixed populations, the authors study two-strategy multi-player symmetric games on the circle. Instead of every individual interacting with its nearest neighbours as assumed in Chapter 2, it interacts with $n-1$ nearest neighbours simultaneously, playing a game with $n-1$ individuals on the left, a game with $n-2$ individuals on the left and one on the right and so on. They find analytically appropriate conditions for one strategy to be favoured over the other in well-known games following the update rules of the IP and the DB-B process (see Chapter 3). One restriction of this model is that although each individual interacts with $n-1$ other individuals, its offspring can replace only an individual next to it. It would be interesting to seek methods for the analysis of the case where any of the $n-1$ individuals that an individual interacts with could be replaced, although this will make the model more complicated. The model could also be considered on other graphs where due to symmetric properties an analytic investigation could be possible, such as the star graph.

Another limitation of the present research work, and in general of a large amount of work where models of evolution in graph structured populations are considered, is that the graph structure is static. This implies that the number of individuals remains constant over time and each individual interacts only with a fixed number of other individuals. In reality, in many populations both the number of individuals and the connectivity of each individual vary with time, and thus the population structure is dynamic and evolves. The development of approximation methods for the study of the evolutionary process on time-evolving graphs is an interesting research topic. Some significant work has been already done in this direction (e.g., Pacheco *et al.*, 2006a,b; Kun and Scheuring, 2009; Poncela *et al.*, 2009; Wu *et al.*, 2010).

So, how have populations evolved and how do they continue to evolve? What are the factors that influence the evolutionary processes? What is the extent of their influence? Mathematics has provided powerful tools to explore theories and arguments, fill the gaps and give answers.

APPENDIX A

Stochastic evolutionary dynamics in finite homogeneous populations

A.1 Fixation probability

The fixation probability of $i \in [1, N-1]$ A individuals in a finite well-mixed population of size N, ${}^{A}P_{i}$, is given by the solution of the system

$$ {}^{A}P_{i} = p_{i,i+1}{}^{A}P_{i+1} + p_{i,i-1}{}^{A}P_{i-1} + (1 - p_{i,i+1} - p_{i,i-1}){}^{A}P_{i},\ 1 \leq i \leq N-1. \tag{A.1} $$

It is assumed that there is no mutation, just selection, that is each offspring is always a perfect copy of its parent, and thus the evolutionary process lasts until one of the types of individuals takes over the population replacing all the individuals of the other type. Hence, the process has two absorbing states; the state where A individuals die out ($i = 0$) and the state where they fixate in the population ($i = N$). At the absorbing states

$$ {}^{A}P_{0} = 0, \tag{A.2} $$

$$ {}^{A}P_{N} = 1. \tag{A.3} $$

Equation (A.1) can be rearranged to

$$ {}^{A}P_{i+1} - {}^{A}P_{i} = q_{i}\left({}^{A}P_{i} - {}^{A}P_{i-1}\right), \tag{A.4} $$

where $q_{i} = p_{i,i-1}/p_{i,i+1}$.
Let $x_{i} = {}^{A}P_{i} - {}^{A}P_{i-1}$. From equation (A.4) we get

$$ x_{i+1} = q_{i}x_{i}. \tag{A.5} $$

We have

$$x_1 = {}^A P_1 - {}^A P_0 = {}^A P_1 \tag{A.6}$$

$$x_2 = {}^A P_2 - {}^A P_1 = q_1 x_1 = q_1 {}^A P_1 \tag{A.7}$$

$$\vdots$$

$$x_N = {}^A P_N - {}^A P_{N-1} = q_{N-1} x_{N-1} = q_1 q_2 \cdots q_{N-2} q_{N-1} {}^A P_1. \tag{A.8}$$

Summing all x_i, $i \in [1,N]$, we obtain

$$\sum_{i=1}^{N} x_i = {}^A P_1 - {}^A P_0 + {}^A P_2 - {}^A P_1 + \cdots + {}^A P_N - {}^A P_{N-1} = {}^A P_N - {}^A P_0 = 1. \tag{A.9}$$

Thus,

$$\sum_{i=1}^{N} x_i = (1 + q_1 + \cdots + q_1 q_2 \cdots q_{N-1}) {}^A P_1 = \left(1 + \sum_{j=1}^{N-1} \prod_{k=1}^{j} q_k\right) {}^A P_1 = 1. \tag{A.10}$$

Hence, the fixation probability of a single A individual in a finite well-mixed population of B individuals is given by

$${}^A P_1 = \frac{1}{1 + \sum_{j=1}^{N-1} \prod_{k=1}^{j} q_k}. \tag{A.11}$$

Similarly, we have

$$\sum_{i=1}^{i} x_i = {}^A P_i \Rightarrow \left(1 + \sum_{j=1}^{i-1} \prod_{k=1}^{j} q_k\right) {}^A P_1 = {}^A P_i. \tag{A.12}$$

Thus, from (A.11) and (A.12), it follows that ${}^A P_i$, $i \in [1,N]$, is given by formula (1.27).

A.2 Mean time to absorption

The mean time to absorption starting from $i \in [1, N-1]$ A individuals in a finite well-mixed population of size N, T_i, is given by the solution of the system

$$T_i = p_{i,i+1}T_{i+1} + p_{i,i-1}T_{i-1} + (1 - p_{i,i+1} - p_{i,i-1})T_i + 1, \ 1 \le i \le N-1, \quad \text{(A.13)}$$

$$T_0 = 0, \quad \text{(A.14)}$$

$$T_N = 0. \quad \text{(A.15)}$$

Equation (A.13) can be written in the form

$$T_{i+1} - T_i = q_i\,(T_i - T_{i-1}) - \frac{1}{p_{i,i+1}}. \quad \text{(A.16)}$$

Following the method of Section A.1, let $y_i = T_i - T_{i-1}$. Then (A.16) is written as

$$y_{i+1} = q_i y_i - \frac{1}{p_{i,i+1}}. \quad \text{(A.17)}$$

We have

$$y_1 = T_1 - T_0 = T_1 \quad \text{(A.18)}$$

$$y_2 = T_2 - T_1 = q_1 y_1 - \frac{1}{p_{1,2}} = q_1 T_1 - \frac{1}{p_{1,2}} \quad \text{(A.19)}$$

$$y_3 = T_3 - T_2 = q_2 y_2 - \frac{1}{p_{2,3}} = q_1 q_2 T_1 - \frac{1}{p_{1,2}} q_2 - \frac{1}{p_{2,3}} \quad \text{(A.20)}$$

$$\vdots$$

$$y_N = T_N - T_{N-1} = q_1 q_2 q_3 \cdots q_{N-1} T_1 - \frac{1}{p_{1,2}} q_2 \cdots q_{N-1} - \frac{1}{p_{2,3}} q_3 \cdots q_{N-1} - \\ - \frac{1}{p_{N-2,N-1}} q_{N-1} - \frac{1}{p_{N-1,N}}. \quad \text{(A.21)}$$

Summing over all y_i, $i \in [1, N]$, we get

$$\sum_{i=1}^{N} y_i = T_1 - T_0 + T_2 - T_1 + \cdots + T_N - T_{N-1} = T_N - T_0 = 0 \quad \text{(A.22)}$$

$$\Rightarrow (1 + q_1 + q_1 q_2 + \cdots + q_1 q_2 q_3 \cdots q_{N-1})\,T_1 - \frac{1}{p_{1,2}} - \frac{1}{p_{2,3}} - \cdots - \\ - \frac{1}{p_{N-1,N}} - \frac{1}{p_{1,2}} q_2 - \cdots - \frac{1}{p_{1,2}} q_2 \cdots q_{N-1} - \cdots - \frac{1}{p_{N-2,N-1}} q_{N-1} = 0. \quad \text{(A.23)}$$

From the equation (A.23) we obtain that the mean time to absorption starting from a single A individual, T_1, is given by

$$T_1 = {}^{A}P \sum_{j=1}^{N-1} \frac{1}{p_{j,j+1}} \sum_{l=j}^{N-1} \prod_{k=j+1}^{l} q_k. \tag{A.24}$$

Similarly,

$$\sum_{i=1}^{i} y_i = T_1 - T_0 + T_2 - T_1 + \cdots + T_i - T_{i-1} = T_i - T_0 = T_i. \tag{A.25}$$

Following the same way, we obtain that the mean time to absorption starting from $i \in [1,N]$ A individuals, T_i, is given by (1.34).

A.3 Mean time to fixation

The fixation time of $i \in [1,N-1]$ A individuals in a finite well-mixed population of size N, ${}^{A}F_i$, is given by the solution of the system

$${}^{A}P_i{}^{A}F_i = p_{i,i+1}{}^{A}P_{i+1}{}^{A}F_{i+1} + p_{i,i-1}{}^{A}P_{i-1}{}^{A}F_{i-1} + (1 - p_{i,i+1} - p_{i,i-1}){}^{A}P_i{}^{A}F_i + {}^{A}P_i, \tag{A.26}$$

$$1 \leq i \leq N-1$$

(see Antal and Scheuring (2006) and Traulsen and Hauert (2009)). The boundary conditions of the system are ${}^{A}P_0{}^{A}F_0 = 0$ because ${}^{A}P_0 = 0$, and ${}^{A}P_N{}^{A}F_N = 0$ because ${}^{A}F_N = 0$.

Let us use the notation ${}^{A}z_i = {}^{A}P_i{}^{A}F_i$. Equation (A.26) can be written as

$${}^{A}z_{i+1} - {}^{A}z_i = q_i({}^{A}z_i - {}^{A}z_{i-1}) - \frac{{}^{A}P_i}{p_{i,i+1}}. \tag{A.27}$$

Following the same method as in Sections A.1 and A.2 we find

$${}^{A}z_1 = \frac{\sum_{j=1}^{N-1} \frac{{}^{A}P_j}{p_{j,j+1}} \sum_{l=j}^{N-1} \prod_{k=j+1}^{l} \frac{p_{k,k-1}}{p_{k,k+1}}}{1 + \sum_{j=1}^{N-1} \prod_{k=1}^{j} \frac{p_{k,k-1}}{p_{k,k+1}}}. \tag{A.28}$$

But ${}^{A}z_1 = {}^{A}P_1 {}^{A}F_1$. Thus, the fixation probability of a single A individual in a finite well-mixed population of B individuals, ${}^{A}F_1$, is given by

$$ {}^{A}F_1 = \sum_{j=1}^{N-1} \frac{{}^{A}p_j}{p_{j,j+1}} \sum_{l=j}^{N-1} \prod_{k=j+1}^{l} \frac{p_{k,k-1}}{p_{k,k+1}}. \tag{A.29} $$

Similarly, we find

$$ \begin{aligned} {}^{A}z_i &= \left(1 + \sum_{j=1}^{i-1} \prod_{k=1}^{j} \frac{p_{k,k-1}}{p_{k,k+1}}\right) {}^{A}z_1 - \sum_{j=1}^{i-1} \frac{{}^{A}p_j}{p_{j,j+1}} \sum_{l=j}^{i-1} \prod_{k=j+1}^{l} \frac{p_{k,k-1}}{p_{k,k+1}} \\ &\overset{(A.28)}{=} {}^{A}P_i \left(\sum_{j=1}^{N-1} \frac{{}^{A}p_j}{p_{j,j+1}} \sum_{l=j}^{N-1} \prod_{k=j+1}^{l} \frac{p_{k,k-1}}{p_{k,k+1}} \right) - \sum_{j=1}^{i-1} \frac{{}^{A}p_j}{p_{j,j+1}} \sum_{l=j}^{i-1} \prod_{k=j+1}^{l} \frac{p_{k,k-1}}{p_{k,k+1}}. \end{aligned} \tag{A.30} $$

Thus, substituting back ${}^{A}z_i = {}^{A}P_i {}^{A}F_i$, we find that the fixation time of $i \in [1, N]$ A individuals, ${}^{A}F_i$, is given by (1.35).

APPENDIX B

Evolutionary dynamics on graphs under various update rules

B.1 Derivation of the transition probabilities on the circle under various update rules

In the BD-D process, the transition probabilities from one state to another on a circle of size N are the following:

$$p_{1,2} = \frac{1}{N}, \tag{B.1}$$

$$p_{2,3} = \frac{2}{N} \cdot \frac{\alpha+\beta}{\alpha+\beta+\gamma+\delta}, \tag{B.2}$$

$$p_{i,i+1} = \frac{2}{N} \cdot \frac{2\alpha}{2\alpha+\gamma+\delta}, \quad 3 \leq i \leq N-2, \tag{B.3}$$

$$p_{N-1,N} = \frac{2}{N} \cdot \frac{\alpha}{\alpha+\gamma}, \tag{B.4}$$

$$p_{1,0} = \frac{2}{N} \cdot \frac{\delta}{\beta+\delta}, \tag{B.5}$$

$$p_{i,i-1} = \frac{2}{N} \cdot \frac{2\delta}{\alpha+\beta+2\delta}, \quad 2 \leq i \leq N-3, \tag{B.6}$$

$$p_{N-2,N-3} = \frac{2}{N} \cdot \frac{\gamma+\delta}{\alpha+\beta+\gamma+\delta}, \tag{B.7}$$

$$p_{N-1,N-2} = \frac{1}{N}. \tag{B.8}$$

In the VM, the transition probabilities between the different states on the circle are given by

$$p_{1,2} = \frac{2\beta\delta}{4\beta\delta + \big((N-3)\beta + \delta\big)(\gamma + \delta)}, \tag{B.9}$$

$$p_{i,i+1} = \frac{2\alpha\delta(\alpha+\beta)}{4\alpha\delta(\alpha+\beta+\gamma+\delta) + \big((N-i-2)\alpha + (i-2)\delta\big)(\alpha+\beta)(\gamma+\delta)}, \tag{B.10}$$

$$2 \leq i \leq N-2,$$

$$p_{N-1,N} = \frac{\alpha(\alpha+\beta)}{4\alpha\gamma + \big(\alpha + (N-3)\gamma\big)(\alpha+\beta)}, \tag{B.11}$$

$$p_{1,0} = \frac{\delta(\gamma+\delta)}{4\beta\delta + \big((N-3)\beta + \delta\big)(\gamma + \delta)}, \tag{B.12}$$

$$p_{i,i-1} = \frac{2\alpha\delta(\gamma+\delta)}{4\alpha\delta(\alpha+\beta+\gamma+\delta) + \big((N-i-2)\alpha + (i-2)\delta\big)(\alpha+\beta)(\gamma+\delta)}, \tag{B.13}$$

$$2 \leq i \leq N-2,$$

$$p_{N-1,N-2} = \frac{2\alpha\gamma}{4\alpha\gamma + \big(\alpha + (N-3)\gamma\big)(\alpha+\beta)}. \tag{B.14}$$

In the DB-B process, the transition probabilities on the circle are given by

$$p_{1,2} = \frac{2}{N} \cdot \frac{\beta}{\beta+\delta}, \tag{B.15}$$

$$p_{i,i+1} = \frac{2}{N} \cdot \frac{\alpha+\beta}{\alpha+\beta+2\delta}, \quad 2 \leq i \leq N-3, \tag{B.16}$$

$$p_{N-2,N-1} = \frac{2}{N} \cdot \frac{\alpha+\beta}{\alpha+\beta+\gamma+\delta}, \tag{B.17}$$

$$p_{N-1,N} = \frac{1}{N}, \tag{B.18}$$

$$p_{1,0} = \frac{1}{N}, \tag{B.19}$$

$$p_{2,1} = \frac{2}{N} \cdot \frac{\gamma+\delta}{\alpha+\beta+\gamma+\delta}, \tag{B.20}$$

$$p_{i,i-1} = \frac{2}{N} \cdot \frac{\gamma+\delta}{2\alpha+\gamma+\delta}, \quad 3 \leq i \leq N-2, \tag{B.21}$$

$$p_{N-1,N-2} = \frac{2}{N} \cdot \frac{\gamma}{\alpha+\gamma}. \tag{B.22}$$

It is observed that the ratio $p_{i,i-1}/p_{i,i+1}$ in the IP and the VM is equal $\forall\ 1 \leq i \leq N-1$. Therefore, the fixation probability of mutants from any state is identical in the two processes. In addition, since the probabilities of having a transition given that the number of mutants either increases or decreases by one in each state are the same in the two processes, the mean number of transitions before absorption and mutants' fixation are also identical. However, the mean time to absorption and fixation are different.

B.2 Derivation of the results in section 3.3

B.2.1 Derivation of $\rho^{\mathrm{S}}_{\mathrm{IP}}$

Substituting the transition probabilities (2.91)–(2.94) into (2.125), we obtain that in the IP the ratio $\rho^{\mathrm{S}}_{\mathrm{IP}}$ is given by

$$\rho^{\mathrm{S}}_{\mathrm{IP}} = y_1(n)y_2(n), \tag{B.23}$$

where

$$y_1(n) = \frac{\beta\big(n^3(n\gamma+\beta)+n^2\beta+(n-1)\delta+\gamma\big)\big(n^2\gamma+(n-1)\alpha+\beta\big)(n\beta+\gamma)}{\gamma\big(n^3(n\beta+\gamma)+n^2\gamma+(n-1)\alpha+\beta\big)\big(n^2\beta+(n-1)\delta+\gamma\big)(n\gamma+\beta)} \tag{B.24}$$

and

$$y_2(n) = \prod_{k=1}^{n-1} \frac{\big(k\alpha+(n-k)\beta\big)\big(n^2\beta+k\gamma+(n-k)\delta\big)}{\big(k\gamma+(n-k)\delta\big)\big(n^2\gamma+k\alpha+(n-k)\beta\big)}. \tag{B.25}$$

We have

$$\lim_{n\to\infty} y_1(n) = 1. \tag{B.26}$$

$y_2(n)$ can be written as

$$y_2(n) = \exp\left(\sum_{k=1}^{n} \ln \frac{\big(k\alpha+(n-k)\beta\big)\big(n^2\beta+k\gamma+(n-k)\delta\big)}{\big(k\gamma+(n-k)\delta\big)\big(n^2\gamma+k\alpha+(n-k)\beta\big)}\right). \tag{B.27}$$

For large n, the above sum can be approached by the following integral

$$\begin{aligned} I &= \int_1^n \left(\ln\left(\frac{x(\alpha-\beta)+n\beta}{n^2\gamma+x(\alpha-\beta)+n\beta}\right) - \ln\left(\frac{x(\gamma-\delta)+n\delta}{n^2\beta+x(\gamma-\delta)+n\delta}\right)\right) dx \\ \Rightarrow I &\approx \frac{n^2\gamma}{\alpha-\beta}\int_{\frac{b}{n\gamma}}^{\frac{a}{n\gamma}} \ln\left(\frac{u}{u+1}\right) du - \frac{n^2\beta}{\gamma-\delta}\int_{\frac{\delta}{n\beta}}^{\frac{\gamma}{n\beta}} \ln\left(\frac{v}{v+1}\right) dv, \quad \alpha\neq\beta,\ \gamma\neq\delta. \end{aligned} \tag{B.28}$$

Evaluating the above integrals we find

$$I \approx n\left(\frac{1}{\alpha-\beta}\big(\alpha\ln\alpha-\beta\ln\beta\big)+\ln\beta-\left(\frac{1}{\delta-\gamma}\big(\delta\ln\delta-\gamma\ln\gamma\big)+\ln\gamma\right)\right) \tag{B.29}$$

$$= \ln\left(\frac{\alpha\beta}{\gamma\delta}\frac{\left(\frac{\alpha}{\beta}\right)^{\frac{\beta}{\alpha-\beta}}}{\left(\frac{\delta}{\gamma}\right)^{\frac{\gamma}{\delta-\gamma}}}\right)^{n}. \tag{B.30}$$

Therefore, from (B.23), (B.26), (B.27) and (B.30) we obtain that for large *n*,

$$\ln(\rho^{\mathrm{S}}_{\mathrm{IP}}) \approx \ln\left(\frac{\alpha\beta}{\gamma\delta}\frac{\left(\frac{\alpha}{\beta}\right)^{\frac{\beta}{\alpha-\beta}}}{\left(\frac{\delta}{\gamma}\right)^{\frac{\gamma}{\delta-\gamma}}}\right)^{n}, \quad \alpha\neq\beta,\ \gamma\neq\delta. \tag{B.31}$$

B.2.2 Derivation of $\rho^{\mathrm{S}}_{\mathrm{BD\text{-}D}}$

Substituting the transition probabilities (3.1)–(3.4) into (2.125), we obtain that in the BD-D process $\rho^{\mathrm{S}}_{\mathrm{BD\text{-}D}}$ is given by

$$\rho^{\mathrm{S}}_{\mathrm{BD\text{-}D}} = y_3(n)y_4(n), \tag{B.32}$$

where

$$y_3(n) = \frac{\big(n(n+1)\big((n-1)\beta+\delta\big)+(n-1)\beta+2\delta\big)\big((n-1)\gamma+2\alpha\big)}{\big(n(n+1)\big((n-1)\gamma+\alpha\big)+(n-1)\gamma+2\alpha\big)\big((n-1)\beta+2\delta\big)} \tag{B.33}$$

and

$$y_4(n) = \prod_{k=1}^{n-1}\frac{\alpha\big((n-k)\beta+(k+1)\delta\big)}{\delta\big((n-k+1)\alpha+k\gamma\big)} = \prod_{k=1}^{n-1}\frac{n+1+k(\beta/\delta-1)}{n+1+k(\gamma/\alpha-1)}. \tag{B.34}$$

We have

$$\lim_{n\to\infty} y_3(n) = 1. \tag{B.35}$$

$y_4(n)$ can be written as

$$y_4(n) = \exp\left(\sum_{k=1}^{n}\ln\frac{n+1+x(\beta/\delta-1)}{n+1+x(\gamma/\alpha-1)}\right). \tag{B.36}$$

For large n, the above sum can be approached by the following integral

$$I = n\int_0^1 \ln\left(\frac{1+x(\beta/\delta-1)}{1+x(\gamma/\alpha-1)}\right) dx. \tag{B.37}$$

Evaluating the above integral we find

$$I = n\left(\frac{\beta}{\delta-\beta}\big(\ln\delta - \ln\beta\big) - \frac{\gamma}{\alpha-\gamma}\big(\ln\alpha - \ln\gamma\big)\right) = \ln\left(\frac{\left(\frac{\delta}{\beta}\right)^{\frac{\beta}{\delta-\beta}}}{\left(\frac{\alpha}{\gamma}\right)^{\frac{\gamma}{\alpha-\gamma}}}\right)^n, \tag{B.38}$$

$$\alpha \neq \gamma,\ \beta \neq \delta.$$

Therefore, from (B.32), (B.35), (B.36) and (B.38) we obtain that for large n,

$$\ln(\rho^{\mathrm{s}}_{\mathrm{BD\text{-}D}}) \approx \ln\left(\frac{\left(\frac{\delta}{\beta}\right)^{\frac{\beta}{\delta-\beta}}}{\left(\frac{\alpha}{\gamma}\right)^{\frac{\gamma}{\alpha-\gamma}}}\right)^n, \quad \alpha \neq \gamma,\ \beta \neq \delta. \tag{B.39}$$

B.2.3 Derivation of $\rho^{\mathrm{s}}_{\mathrm{VM}}$

Substituting the transition probabilities (3.5)–(3.8) into (2.125), we obtain that in the VM $\rho^{\mathrm{s}}_{\mathrm{VM}}$ is given by

$$\rho^{\mathrm{s}}_{\mathrm{VM}} = y_5(n)y_6(n), \tag{B.40}$$

where

$$y_5(n) = \frac{\beta\big((n+1)\beta+(n-1)\delta+2\gamma\big)\big((n-1)\alpha+\beta+\gamma\big)(n\gamma+\beta)}{\gamma\big((n+1)\gamma+(n-1)\alpha+2\beta\big)\big((n-1)\delta+\beta+\gamma\big)(n\beta+\gamma)} \tag{B.41}$$

and

$$y_6(n) = \prod_{k=1}^{n-1}\frac{\big(k\alpha+(n-k)\beta\big)\big(k\gamma+(n-k)\delta+\beta\big)}{\big(k\gamma+(n-k)\delta\big)\big(k\alpha+(n-k)\beta+\gamma\big)}. \tag{B.42}$$

We have

$$\lim_{n\to\infty} y_5(n) = \frac{\alpha(\beta+\delta)}{\delta(\gamma+\alpha)}. \tag{B.43}$$

$y_6(n)$ can be written as

$$y_6(n) = \exp\left(\sum_{k=1}^{n}\ln\frac{\big(k\alpha+(n-k)\beta\big)\big(k\gamma+(n-k)\delta+\beta\big)}{\big(k\gamma+(n-k)\delta\big)\big(k\alpha+(n-k)\beta+\gamma\big)}\right). \tag{B.44}$$

For large *n*, the above sum is approached by the following integral

$$I = n\int_0^1 \left(\ln\left(\frac{x(\alpha-\beta)+\beta}{x(\alpha-\beta)+\beta+\gamma/n}\right) - \ln\left(\frac{x(\gamma-\delta)+\delta}{x(\gamma-\delta)+\delta+\beta/n}\right)\right) dx. \tag{B.45}$$

Evaluating the integral we find

$$I \approx \frac{\gamma}{\beta-\alpha}\big(\ln\alpha-\ln\beta\big) - \frac{\beta}{\gamma-\delta}\big(\ln\delta-\ln\gamma\big) = \ln\frac{\left(\frac{\alpha}{\beta}\right)^{\frac{\gamma}{\beta-\alpha}}}{\left(\frac{\delta}{\gamma}\right)^{\frac{\beta}{\gamma-\delta}}}, \quad \alpha\neq\beta,\ \gamma\neq\delta. \tag{B.46}$$

Therefore, from (B.40), (B.43), (B.44) and (B.46) we obtain that for large *n*,

$$\rho^{\mathrm{s}}_{\mathrm{VM}} \approx \frac{\alpha(\beta+\delta)}{\delta(\gamma+\alpha)}\frac{\left(\frac{\alpha}{\beta}\right)^{\frac{\gamma}{\beta-\alpha}}}{\left(\frac{\delta}{\gamma}\right)^{\frac{\beta}{\gamma-\delta}}}, \quad \alpha\neq\beta,\ \gamma\neq\delta. \tag{B.47}$$

B.2.4 Derivation of $\rho^{\mathrm{s}}_{\mathrm{DB\text{-}B}}$

Substituting the transition probabilities (3.9)–(3.12) into (2.125), we obtain that in the DB-B $\rho^{\mathrm{s}}_{\mathrm{DB\text{-}B}}$ is given by

$$\rho^{\mathrm{s}}_{\mathrm{DB\text{-}B}} = y_7(n)y_8(n), \tag{B.48}$$

where

$$y_7(n) = \frac{\big((n+3)\beta+(n-1)\delta\big)\big((n-1)\alpha+2\gamma\big)}{\big((n+3)\gamma+(n-1)\alpha\big)\big((n-1)\delta+2\beta\big)} \tag{B.49}$$

and

$$y_8(n) = \prod_{k=1}^{n-1}\frac{\big(k\alpha+(n-k)\gamma\big)\big((k+1)\beta+(n-k)\delta\big)}{\big(k\alpha+(n-k+1)\gamma\big)\big(k\beta+(n-k)\delta\big)}. \tag{B.50}$$

We have

$$\lim_{n\to\infty} y_7(n) = \frac{\alpha(\beta+\delta)}{\delta(\gamma+\alpha)}. \tag{B.51}$$

$y_8(n)$ can be written as

$$y_8(n) = \exp\left(\sum_{k=1}^{n}\ln\frac{\big(k\alpha+(n-k)\gamma\big)\big((k+1)\beta+(n-k)\delta\big)}{\big(k\alpha+(n-k+1)\gamma\big)\big(k\beta+(n-k)\delta\big)}\right), \tag{B.52}$$

where for large *n* the above sum can be approached by the following integral

$$I = n\int_0^1 \left(\ln\left(\frac{x(\alpha-\gamma)+\gamma}{x(\alpha-\gamma)+(1+1/n)\gamma}\right) - \ln\left(\frac{x(\beta-\delta)+\delta}{x(\beta-\delta)+\delta+\beta/n}\right)\right) dx. \tag{B.53}$$

Evaluating the integral we find

$$I \approx \frac{\gamma}{\gamma-\alpha}\big(\ln\alpha - \ln\gamma\big) - \frac{\beta}{\beta-\delta}\big(\ln\delta - \ln\beta\big) = \ln \frac{\left(\frac{\alpha}{\gamma}\right)^{\frac{\gamma}{\gamma-\alpha}}}{\left(\frac{\delta}{\beta}\right)^{\frac{\beta}{\beta-\delta}}}, \quad \alpha \neq \gamma,\ \beta \neq \delta. \tag{B.54}$$

Therefore, from (B.48), (B.51), (B.52) and (B.54) we obtain that for large *n*,

$$\rho^{\mathrm{S}}_{\text{DB-B}} \approx \frac{\alpha(\beta+\delta)}{\delta(\gamma+\alpha)} \frac{\left(\frac{\alpha}{\gamma}\right)^{\frac{\gamma}{\gamma-\alpha}}}{\left(\frac{\delta}{\beta}\right)^{\frac{\beta}{\beta-\delta}}}, \quad \alpha \neq \gamma,\ \beta \neq \delta. \tag{B.55}$$

B.2.5 Proposition

In the BD-D and DB-B processes, $\rho^{\mathrm{s}}_{\text{BD-D}} \gtreqless 1 \Leftrightarrow \alpha\beta \gtreqless \gamma\delta,\ \forall\, n$, and $\rho^{\mathrm{s}}_{\text{DB-B}} \gtreqless 1 \Leftrightarrow \alpha\beta \gtreqless \gamma\delta,\ \forall\, n$.

Proof

In the BD-D process, (B.32) can be written in the form

$$\rho^{\mathrm{S}}_{\text{BD-D}} = \frac{f_{\text{BD-D}}\left(\frac{\beta}{\delta}\right)}{f_{\text{BD-D}}\left(\frac{\gamma}{\alpha}\right)}, \tag{B.56}$$

where

$$f_{\text{BD-D}}(x) = \big(2 + n(n+1) + \big(n(n+1)+1\big)(n-1)x\big)(n+x)\prod_{k=2}^{n-2}\big(n + k(x-1) + 1\big). \tag{B.57}$$

$f_{\text{BD-D}}(x)$ is a monotonically increasing function. Hence,

$$\rho^{\mathrm{S}}_{\text{BD-D}} \gtreqless 1 \Leftrightarrow \frac{\beta}{\delta} \gtreqless \frac{\gamma}{\alpha} \Leftrightarrow \alpha\beta \gtreqless \gamma\delta,\ \forall\, n. \tag{B.58}$$

Similarly, in the DB-B process, (B.48) can be written in the form,

$$\rho^{\mathrm{S}}_{\text{DB-B}} = \frac{f_{\text{DB-B}}\left(\frac{\gamma}{\alpha}\right)}{f_{\text{DB-B}}\left(\frac{\beta}{\delta}\right)}, \tag{B.59}$$

where

$$f_{\text{DB-B}}(x) = \frac{2x+n-1}{(n+3)x+n-1}\prod_{k=1}^{n-1}\frac{n+k(x-1)}{n-k+(k+1)x}. \tag{B.60}$$

$f_{\text{DB-B}}(x)$ is a monotonically decreasing function. Hence,

$$\rho^{\mathrm{S}}_{\text{DB-B}} \gtreqless 1 \Leftrightarrow \frac{\beta}{\delta} \gtreqless \frac{\gamma}{\alpha} \Leftrightarrow \alpha\beta \gtreqless \gamma\delta,\ \forall\, n. \tag{B.61}$$

B.3 Derivation of the results in section 3.4

B.3.1 Approximation of ${}^{A}P_{\text{IP}}$ in a large population

Substituting the transition probabilities in the IP, (2.91)–(2.94), into (2.23) we obtain

$$ {}^{A}P_{\text{IP}} = \frac{\frac{1}{n+1}\left(\frac{n^3\beta}{n^2\beta+(n-1)\delta+\gamma}+\frac{\beta}{n\gamma+\beta}\right)}{1+\sum\limits_{j=1}^{n-1}\frac{n^2\gamma}{n^2\gamma+j\alpha+(n-j)\beta}\prod\limits_{k=1}^{j}\frac{(k\gamma+(n-k)\delta)\big(n^2\gamma+k\alpha+(n-k)\beta\big)}{(k\alpha+(n-k)\beta)\big(n^2\beta+k\gamma+(n-k)\delta\big)}}. \tag{B.62}$$

The product in (B.62) can be written as

$$\exp\left(\sum_{k=1}^{j}\ln\frac{\big(k\gamma+(n-k)\delta\big)\big(n^2\gamma+k\alpha+(n-k)\beta\big)}{\big(k\alpha+(n-k)\beta\big)\big(n^2\beta+k\gamma+(n-k)\delta\big)}\right). \tag{B.63}$$

For large *n*, the sum in (B.63) can be approached by the following integral

$$I = n\int_0^z \ln\left(\frac{n\gamma}{\beta}\frac{1}{1+x\frac{\alpha-\beta}{\beta}}+1\right)dx - n\int_0^z \ln\left(\frac{n\beta}{\delta}\frac{1}{1+x\frac{\gamma-\delta}{\delta}}+1\right)dx,\ z=j/n. \tag{B.64}$$

Evaluating the integral we find that for large *n*,

$$I = \ln\big(W_{\text{IP}}(z)\big)^n, \tag{B.65}$$

where

$$W_{\text{IP}}(z) = \left(\frac{\gamma\delta}{\beta^2}\right)^z \frac{\left(1+\frac{\gamma-\delta}{\delta}z\right)^{\left(\frac{\delta}{\gamma-\delta}+z\right)}}{\left(1+\frac{\alpha-\beta}{\beta}z\right)^{\left(\frac{\beta}{\alpha-\beta}+z\right)}},\quad \alpha\neq\beta,\ \gamma\neq\delta. \tag{B.66}$$

From (B.62), (B.63) and (B.65) we obtain that for large *n*, ${}^{A}P_{\text{IP}}$ can be approached by

$$ {}^{A}P_{\text{IP}} = \frac{1}{\sum\limits_{j=0}^{n-1}\big(W_{\text{IP}}(z)\big)^n}. \tag{B.67}$$

In a Hawk–Dove type game, $\beta^2 > \gamma\delta$. If $W_{\text{IP}}(1) > 1$, i.e if $\alpha\beta\left(\frac{\alpha}{\beta}\right)^{\frac{\beta}{\alpha-\beta}} <$

$\gamma\delta\left(\frac{\delta}{\gamma}\right)^{\frac{\gamma}{\delta-\gamma}}$ (which is equivalent to $\rho^{\mathrm{S}}_{\mathrm{IP}} < 1$) then $W_{\mathrm{IP}}(z)$ takes its maximum value when $z = 1$. In this case,

$$^{H}P_{\mathrm{IP}} = \frac{1}{\big(W_{\mathrm{IP}}(1)\big)^{n}} \approx 0. \tag{B.68}$$

If $W_{\mathrm{IP}}(1) < 1$, i.e if $\alpha\beta\left(\frac{\alpha}{\beta}\right)^{\frac{\beta}{\alpha-\beta}} > \gamma\delta\left(\frac{\delta}{\gamma}\right)^{\frac{\gamma}{\delta-\gamma}}$ (which is equivalent to $\rho^{\mathrm{S}}_{\mathrm{IP}} > 1$) then $W_{\mathrm{IP}}(z)$ takes its maximum value when $z = 0$. In this case,

$$^{H}P_{\mathrm{IP}} = \frac{1}{\sum\limits_{j=0}^{n-1}\left(\frac{\gamma\delta}{\beta^2}\right)^{j}} = \frac{1-\frac{\gamma\delta}{\beta^2}}{1-\left(\frac{\gamma\delta}{\beta^2}\right)^{n}} \approx 1-\frac{\gamma\delta}{\beta^2}. \tag{B.69}$$

Following the same procedure in the constant fitness case, we find that for large n the fixation probability of a single mutant, $^{A}P_{\mathrm{IP}}$, is given by

$$^{A}P_{\mathrm{IP}} = \frac{1}{\sum\limits_{j=0}^{n-1}\left(\frac{1}{r^2}\right)^{j}} = \frac{1-\frac{1}{r^2}}{1-\frac{1}{r^{2n}}},\ r \neq 1. \tag{B.70}$$

For $r = 1$, $^{A}P_{\mathrm{IP}} = 1/(n+1)\ \forall\ n$ and thus for large n, $^{A}P_{\mathrm{IP}} \approx 0$.

B.3.2 Approximation of $^{A}P_{\mathrm{BD\text{-}D}}$ in a large population

Substituting the transition probabilities in the BD-D process, (3.1)–(3.4), into (2.23) we obtain

$$^{A}P_{\mathrm{BD\text{-}D}} = \frac{\frac{1}{n+1}\left(\frac{1}{n+1}+\frac{n((n-1)\beta+\delta)}{(n-1)\beta+2\delta}\right)}{1+\sum\limits_{j=1}^{n-1}\frac{(n-j)\alpha+j\gamma}{(n-j+1)\alpha+j\gamma}\prod\limits_{k=1}^{j}\frac{\delta((n-k+1)\alpha+k\gamma)}{\alpha((n-k)\beta+(k+1)\delta)}}. \tag{B.71}$$

The product in (B.71) can be written as

$$\prod_{k=1}^{j}\frac{\delta\big(n+1+k\big(\frac{\gamma}{\alpha}-1\big)\big)}{\beta\big(n+\frac{\delta}{\beta}+k\big(\frac{\delta}{\beta}-1\big)\big)} = \exp\left(\sum_{k=1}^{j}\ln\frac{\delta\big(n+1+k\big(\frac{\gamma}{\alpha}-1\big)\big)}{\beta\big(n+\frac{\delta}{\beta}+k\big(\frac{\delta}{\beta}-1\big)\big)}\right). \tag{B.72}$$

For large n, the sum in (B.72) can be approached by the following integral

$$I = n\int_{0}^{z}\ln\left(\frac{\delta}{\beta}\frac{1+x\big(\frac{\gamma}{\alpha}-1\big)}{1+x\big(\frac{\delta}{\beta}-1\big)}\right)dx,\ z = j/n. \tag{B.73}$$

Evaluating the integral we find that for large n,

$$I = \ln\big(W_{\text{BD-D}}(z)\big)^{n}, \tag{B.74}$$

where

$$W_{\text{BD-D}}(z) = \left(\frac{\delta}{\beta}\right)^{z} \frac{\left(1+\frac{\gamma-\alpha}{\alpha}z\right)^{\left(\frac{\alpha}{\gamma-\alpha}+z\right)}}{\left(1+\frac{\delta-\beta}{\beta}z\right)^{\left(\frac{\beta}{\delta-\beta}+z\right)}}, \quad \alpha \neq \gamma,\ \beta \neq \delta. \tag{B.75}$$

From (B.71), (B.72) and (B.74) we obtain that for large n, ${}^{A}P_{\text{BD-D}}$ can be approached by

$${}^{A}P_{\text{BD-D}} = \frac{1}{\sum\limits_{j=0}^{n-1}\big(W_{\text{BD-D}}(z)\big)^{n}}. \tag{B.76}$$

In a Hawk–Dove type game, $\beta > \delta$. If $W_{\text{BD-D}}(1) > 1$, i.e if $\left(\frac{\delta}{\beta}\right)^{\frac{\beta}{\delta-\beta}} < \left(\frac{\alpha}{\gamma}\right)^{\frac{\gamma}{\alpha-\gamma}}$ (which is equivalent to $\rho^{\text{S}}_{\text{BD-D}} < 1$) then $W_{\text{BD-D}}(z)$ takes its maximum value when $z = 1$. In this case,

$${}^{H}P_{\text{BD-D}} = \frac{1}{\big(W_{\text{BD-D}}(1)\big)^{n}} \approx 0. \tag{B.77}$$

If $W_{\text{BD-D}}(1) < 1$, i.e if $\left(\frac{\delta}{\beta}\right)^{\frac{\beta}{\delta-\beta}} > \left(\frac{\alpha}{\gamma}\right)^{\frac{\gamma}{\alpha-\gamma}}$ (which is equivalent to $\rho^{\text{S}}_{\text{BD-D}} > 1$) then $W_{\text{BD-D}}(z)$ takes its maximum value when $z = 0$. In this case,

$${}^{H}P_{\text{BD-D}} = \frac{1}{\sum\limits_{j=0}^{n-1}\left(\frac{\delta}{\beta}\right)^{j}} = \frac{1-\frac{\delta}{\beta}}{1-\left(\frac{\delta}{\beta}\right)^{n}} \approx 1 - \frac{\delta}{\beta}. \tag{B.78}$$

In our examples, α might become equal to γ. Hence, it remains to consider the case where $\alpha = \gamma$.
From (B.73), for $\alpha = \gamma$, we get

$$I = n\int_{0}^{z} \ln\left(\frac{\delta}{\beta}\frac{1}{1+x\left(\frac{\delta}{\beta}-1\right)}\right) dx,\ z = j/n. \tag{B.79}$$

Evaluating the above integral we find that for large n,

$$I = \ln\big(W'_{\text{BD-D}}(z)\big)^{n}, \tag{B.80}$$

where

$$W'_{\text{BD-D}}(z) = \left(\frac{\delta}{\beta}\right)^{z} \frac{e^{z}}{\left(1+\frac{\delta-\beta}{\beta}z\right)^{\left(\frac{\beta}{\delta-\beta}+z\right)}}. \tag{B.81}$$

Therefore, for large n, the ${}^{A}P_{\text{BD-D}}$ in this case is approached by

$${}^{A}P_{\text{BD-D}} = \frac{1}{\sum\limits_{j=0}^{n-1}\left(W'_{\text{BD-D}}(z)\right)^{n}}. \tag{B.82}$$

Since $\beta > \delta$, $W'_{\text{BD-D}}(1)$ is always less than 1, i.e. $\left(\frac{\delta}{\beta}\right)^{\frac{\beta}{\delta-\beta}} > e$, and $W'_{\text{BD-D}}(z)$ takes its maximum value when $z = 0$. Thus, in this case, the fixation probability is approached by (B.78). Note that, following the same method as in Appendix B.2.2, we find that for $\alpha = \gamma$, $\ln(\rho^{\text{S}}_{\text{BD-D}}) \approx \ln\left(\left(\frac{\delta}{\beta}\right)^{\frac{\beta}{\delta-\beta}} \Big/ e\right)^{n}$. Therefore, in this case, mutant Hawks are always favoured over Doves.

In the constant fitness case, from (B.76) we obtain that for large n, ${}^{A}P_{\text{BD-D}}$ is approached by

$${}^{A}P_{\text{BD-D}} = \frac{1}{\sum\limits_{j=0}^{n-1}\left(\frac{1}{r}\right)^{j}} = \frac{1-\frac{1}{r}}{1-\frac{1}{r^{n}}},\ r \neq 1. \tag{B.83}$$

For $r = 1$, ${}^{A}P_{\text{BD-D}} = 1/(n+1)\ \forall\ n$ and thus for large n, ${}^{A}P_{\text{BD-D}} \approx 0$.

B.3.3 ${}^{A}P_{\text{VM}}$ and ${}^{A}P_{\text{DB-B}}$ in a large population

In the VM,

$${}^{A}P_{\text{VM}} < \frac{1}{n+1}\left(\pi^{AA}_{0,1} + n\pi^{BA}_{1,1}\right) = \frac{n\beta}{n+1}\left(\frac{1}{n\beta+\gamma} + \frac{1}{n\delta+\beta+\gamma-\delta}\right). \tag{B.84}$$

In a Hawk–Dove game, since $\beta > \delta$,

$${}^{H}P_{\text{VM}} < \frac{1}{n+1}\left(\frac{\beta+\delta}{\delta}\right). \tag{B.85}$$

In the constant fitness case,

$${}^{A}P_{\text{VM}} < \frac{r+1}{n+1},\ \forall\ r. \tag{B.86}$$

In the DB-B process,

$$^{A}P_{\text{DB-B}} < \frac{1}{n+1}\left(\pi_{0,1}^{AA} + n\pi_{1,1}^{BA}\right) = \frac{n}{n+1}\left(\frac{1}{n+1} + \frac{\beta}{n\delta + 2\beta - \delta}\right). \tag{B.87}$$

In a Hawk–Dove game, as in the VM,

$$^{H}P_{\text{DB-B}} < \frac{1}{n+1}\left(\frac{\beta+\delta}{\delta}\right). \tag{B.88}$$

In the constant fitness case, for $r \geq 1/2$

$$^{A}P_{\text{DB-B}} < \frac{r+1}{n+1}, \tag{B.89}$$

while for $r < 1/2$,

$$^{A}P_{\text{DB-B}} < \frac{r+1}{n-1}. \tag{B.90}$$

Therefore, $\forall\, r$, $^{A}P_{\text{DB-B}} < \frac{r+1}{n-1}$.
Hence, both in the VM and the DB-B process, the average fixation probability of a single mutant decreases to 0 as n increases to infinity.

Note that in the case where a mutant Dove invades into a population of Hawks, all the above results can be obtained by exchanging α and δ, and β and γ.

APPENDIX C

Food sharing in kleptoparasitic populations

C.1 The optimal strategy is always pure

In the model considered, there are 21 possible groups of strategies that an animal can play, 6 of which consist of pure strategies and 15 of mixed strategies. These are summarised in Table C.1.

Strategies denoted by (*) in Table C.1 are strategies with $p_2 = 0$, that is, strategies where animals never share their food. In this case, the model reduces to the model considered in Broom *et al*. (2004). In this paper, the authors have shown that the mean time required for a searcher animal that has just encountered a handler to consume a food item is a strictly monotonic function (except with the possible exception of a non-generic parameter set, see below) of the probability with which the searcher attacks the handler, p_1. Therefore, depending on the parameter values, the searcher animal minimises the time it needs for the consumption of a food item by playing either $p_1 = 0$ or $p_1 = 1$. Any other strategy $0 < p_1 < 1$ results in a higher expected time and thus cannot be evolutionarily stable. Similarly, it has been shown that the average time needed for a handler to consume a food item after being attacked by a searcher is either a strictly increasing or a strictly decreasing function of p_3 and therefore the optimal strategy is always either $p_3 = 0$ or $p_3 = 1$, depending on the parameter values.

Strategies denoted by (**) are the two additional pure strategies to the model of Broom *et al*. (2004) where $p_2 = 1$, i.e. the strategies where animals always share their food when other animals attack. It has been shown in Chapter 6 that under certain conditions one of these can be an ESS, the other not.

In the case where none of the animals of the population behave aggressively, i.e.

Table C.1: Possible ESSs. Strategies denoted by * are strategies with $p_2 = 0$, strategies denoted by ** are pure strategies with $p_2 = 1$, and strategies denoted by *** are strategies with $p_1 = 0$ and $0 < p_2 < 1$

		Strategy at the handling state, p_2, p_3						
		$p_2=1$ $p_3=0$	$p_2=0$ $p_3=1$	$p_2=p_3=0$	$p_2=0$ $0<p_3<1$	$0<p_2<1$ $p_3=0$	$0<p_2<1$ $0<p_3<1$ $p_2+p_3=1$	$0<p_2<1$ $0<p_3<1$ $p_2+p_3<1$
Strategy at the searching state, p_1	$p_1=0$	**	*	*	*	***	***	***
	$0<p_1<1$	S 1	*	*	*	S 2	S 4	S 6
	$p_1=1$	**	*	*	*	S 3	S 5	S 7

$p_1 = q_1 = 0$ (strategies denoted by (***) in Table C.1 are such strategies where $0 < p_2 < 1$), the average time required for an attacked mutant handler that plays strategy $(0, q_2, q_3)$ to consume a food item, T^*_{HA}, is a function of the form (see equation (6.28))

$$T^*_{\text{HA}} = c_1 q_2 + c_2 q_3 + c_3, \tag{C.1}$$

where c_1, c_2 and c_3 depend only on the parameters of the model $t_a, t_h, t_c, \nu_f f$ and α. Hence, if the values of the parameters are such that c_1 and c_2 are both greater than zero, then the optimal strategy for the mutant is $q_2 = q_3 = 0$. In any other case, if $c_1 < c_2$, the optimal strategy is $q_2 = 1$ and $q_3 = 0$, whereas if $c_1 > c_2$ the optimal strategy is $q_2 = 0$ and $q_3 = 1$.

It remains to consider whether any of the strategies (S 1)–(S 7) is an ESS. Due to the complexity of the mathematical formulae, an analytic investigation is very difficult. Hence, we consider whether each of the remaining strategies is an ESS mainly through extensive numerical investigation.

Regarding strategies (S 1), from equation (6.18) we get that in a population that plays strategy $(0 < p_1 < 1, 1, 0)$,

$$T^*_{\text{SA}}(0,1,0) = T^*_{\text{S}}(0,1,0), \tag{C.2}$$

while

$$T^*_{\text{SA}}(1,1,0) = T^*_{\text{C}}(1,1,0) = t_c + \frac{T^*_{\text{S}}(1,1,0)}{2} \tag{C.3}$$

($T_{\text{X}}(p_1, p_2, p_3)$ denotes the average time required for an animal at state X to consume a food item when playing strategy (p_1, p_2, p_3)). If there is any equilibrium strategy $(p^*_1, 1, 0)$ in (S 1), then $T_{\text{SA}}(p^*_1, 1, 0)$ should be equal to $T^*_{\text{SA}}(0,1,0)$ and $T^*_{\text{SA}}(1,1,0)$. But when $T^*_{\text{SA}}(0,1,0) = T^*_{\text{SA}}(1,1,0)$, then $T^*_{\text{S}}(0,1,0) = T^*_{\text{S}}(1,1,0)$. Hence, equating equations (C.2) and (C.3), we get

$$T_{\mathrm{S}}^{*}(0,1,0) = T_{\mathrm{S}}^{*}(1,1,0) = T_{\mathrm{S}}(p_1^{*},1,0) = 2t_c. \tag{C.4}$$

On the other hand, if the strategy $(p_1^{*},1,0)$ is an equilibrium strategy, then it cannot be invaded by the mutant strategy $(p_1^{*},0,0)$, i.e. the average required time for the mutant handler that has just been attacked in a population that plays strategy $(p_1^{*},1,0)$, $T_{\mathrm{HA}}^{*}(p_1^{*},0,0)$, is higher than the average time required when playing the population strategy, $T_{\mathrm{HA}}(p_1^{*},1,0)$. Using equation (6.24) we find that

$$T_{\mathrm{HA}}^{*}(p_1^{*},0,0) > T_{\mathrm{HA}}(p_1^{*},1,0) \tag{C.5}$$

$$\Rightarrow T_{\mathrm{S}}^{*}(p_1^{*},0,0) > T_{\mathrm{C}}(p_1^{*},1,0) \Rightarrow T_{\mathrm{S}}^{*}(p_1^{*},0,0) = T_{\mathrm{S}}(p_1^{*},1,0) > 2t_c. \tag{C.6}$$

This contradicts (C.4). Consequently, there is not any equilibrium strategy $(0 < p_1 < 1,1,0)$. This is also verified from the results of numerical examples for a wide range of parameter values (see Figure C.1a for an example).

In a similar way it is proved that there is no equilibrium strategy in the class of strategies (S 6). If there was an equilibrium strategy $(0 < p_1^{*} < 1, 0 < p_2^{*} < 1, 0 < p_3^{*} < 1)$, $p_2^{*}+p_3^{*} < 1$, then $T_{\mathrm{HA}}^{*}(p_1^{*},0,0)$, $T_{\mathrm{HA}}^{*}(p_1^{*},1,0)$ and $T_{\mathrm{HA}}^{*}(p_1^{*},0,1)$ should all be identical, otherwise one of the strategies $(p_1^{*},0,0)$, $(p_1^{*},1,0)$, $(p_1^{*},0,1)$ could invade $(p_1^{*},p_2^{*},p_3^{*})$. In this case, using equations (6.24) and (6.25) we find that

$$T_{\mathrm{S}}(p_1^{*},p_2^{*},p_3^{*}) - T_{\mathrm{H}}(p_1^{*},p_2^{*},p_3^{*}) = \frac{1}{1-\alpha}\frac{t_a}{2}. \tag{C.7}$$

On the other hand, if $(p_1^{*},p_2^{*},p_3^{*})$ is an equilibrium strategy, then $T_{\mathrm{SA}}^{*}(p_1^{*},p_2^{*},p_3^{*}) = T_{\mathrm{SA}}^{*}(1,p_2^{*},p_3^{*}) = T_{\mathrm{SA}}^{*}(0,p_2^{*},p_3^{*})$ which yields that

$$T_{\mathrm{SA}}^{*}(1,p_2^{*},p_3^{*}) = T_{\mathrm{S}}^{*}(0,p_2^{*},p_3^{*}) = T_{\mathrm{S}}^{*}(1,p_2^{*},p_3^{*}) = T_{\mathrm{S}}^{*}(p_1^{*},p_2^{*},p_3^{*}). \tag{C.8}$$

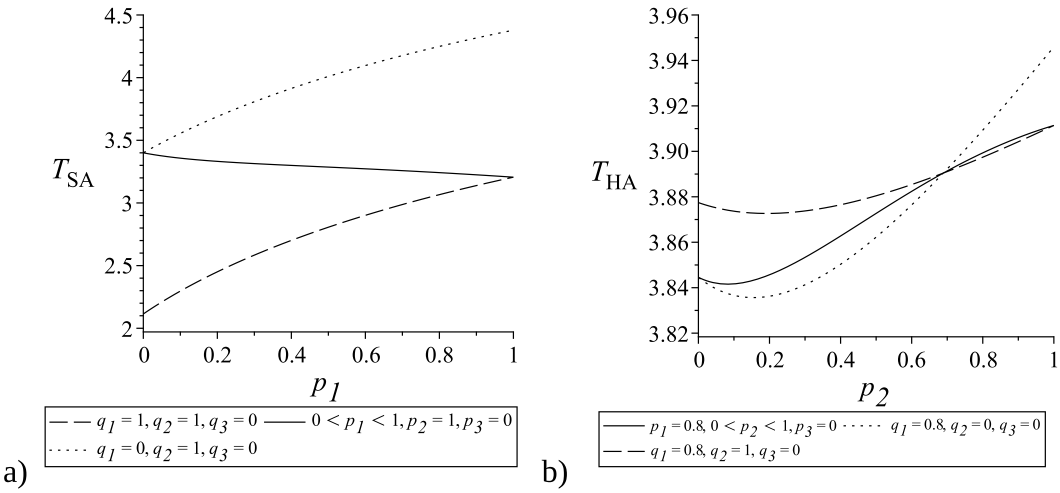
Substituting into equation (6.20) we obtain that

$$T_{\mathrm{S}}^{*}(p_1^{*},p_2^{*},p_3^{*}) - T_{\mathrm{H}}^{*}(p_1^{*},p_2^{*},p_3^{*}) = \frac{1}{\nu_f f}. \tag{C.9}$$

Hence, if a strategy of the (S 6) class is an equilibrium strategy, then (C.7) and (C.9) must hold. This leads to

$$1-\alpha = \nu_f f \frac{t_a}{2}, \tag{C.10}$$

i.e. that the probability of a challenger losing a fight is equal to the ratio of the expected duration of the fight and the mean time searching for food. These are all



a) b)

Figure C.1: (a) The expected time until the consumption of a food item of searcher animals playing strategies $(1,1,0)$, $(0,1,0)$ and $(0 < p_1 < 1,1,0)$ in a population playing strategy $(0 < p_1 < 1,1,0)$ for the example considered in Figure 6.3b for $t_a/2 = 1$ and $t_c = 2$. Numerical examples indicate that in every population which adopts a strategy $(0 < p_1 < 1,1,0)$, a mutant animal that plays either strategy $(0,1,0)$ or strategy $(1,1,0)$ always does better than any other animal that uses the population strategy. Thus, such populations can be invaded by those mutant strategies and as a result, strategies $(0 < p_1 < 1,1,0)$ cannot be ESSs. (b) The expected time until the consumption of a food item of handler animals playing strategies $(0.8,1,0)$, $(0.8,0,0)$ and $(0.8, 0 < p_2 < 1,0)$ in a population playing strategy $(0.8, 0 < p_2 < 1,0)$ for $t_a/2 = 1, t_h = 3, t_c = 2, \nu_f f = 1, \nu_h = 1.5, \alpha = 0.3, P = 1$. An equilibrium strategy $(0 < p_1 \leq 1, 0 < p_2 < 1, 0)$ cannot be evolutionarily stable.

biologically-determined parameters, and we assume that the chance of their precise coincidence in this way is negligible (i.e. the case is non-generic). Thus, for example, such a case would correspond to a region of zero area in a figure such as Figure 6.3, equivalent to the boundary lines.

Numerical investigation also indicates that mixed strategies in the classes (S 4), (S 5) and (S 7) are always invaded and so there are no mixed ESSs in these classes.

Concerning strategies (S 2) and (S 3), numerical examples on a wide range of parameter values also imply that for every value of p_2, $0 < p_2 < 1$, strategies $(0 < p_1 < 1, p_2, 0)$ can always be invaded either by strategy $(0, p_2, 0)$ or by strategy $(1, p_2, 0)$. On the other hand, numerical examples indicate that for given p_1^*, $0 < p_1^* \leq 1$, there is a strategy p_2^*, $0 < p_2^* < 1$, such that for specific values of parameters all the invading strategies $(p_1^*, 0 \leq q_2 \leq 1, 0)$ do equally well in a population playing $(p_1^*, p_2^*, 0)$, i.e. $T_{\mathrm{HA}}(p_1^*, p_2^*, 0) = T_{\mathrm{HA}}^*(p_1^*, 0 \leq q_2 \leq 1, 0)$, whereas any other strategy does worse. Any other population playing a different strategy $(p_1^*, 0 < p_2 < 1, 0)$, $p_2 \neq p_2^*$, can be invaded either by the strategy $(p_1^*, 0, 0)$ or the strategy $(p_1^*, 1, 0)$ (see Figure C.1b for an example). However, in a population that plays a strategy $(p_1, 0 \leq q_2 \leq 1, 0)$, the required time for an attacked handler playing the population strategy, $T_{\mathrm{HA}}(p_1, 0 \leq q_2 \leq 1, 0)$, is less than that required by an attacked handler playing $(p_1^*, p_2^*, 0)$. In other words, if an infinitesimal portion of the population deviates from the equilibrium strategy, evolution will drive the population away from that equilibrium. Thus, according to the second condition of Maynard Smith and Price (1973) for a strategy to be an ESS (see Section 1.2.1), the strategy $(p_1^*, p_2^*, 0)$ cannot be ESS. Hence, none of the strategies (S 2) and (S 3) can be evolutionarily stable.

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