



university of  
groningen

faculty of mathematics  
and natural sciences

# A Spatial Simulation of the Battle of the Sexes

Master's thesis

27th August 2012

Student: Ivar H.J. Postma

Primary supervisor: Dr. M.H.F. Wilkinson

Secondary supervisor: Dr. H. Bekker



# **A Spatial Simulation of the Battle of the Sexes**

Version 1.1

**Ivar H. J. Postma**

Master's thesis Computing Science  
School for Computing and Cognition  
Faculty of Mathematics and Natural Sciences  
University of Groningen



The problem is all inside your head she said to me  
The answer is easy if you take it logically

- *Paul Simon, from: '50 Ways to Leave Your Lover'*



---

---

## Abstract

In many species of animal, females require males to invest a substantial amount of time or effort in a relationship before mating. In evolutionary biology, the Battle of the Sexes is a game-theoretical model that tries to illustrate how this coy behaviour by females can survive over time. In its classical form of the game, the success of a specific mating strategy depends on the ratio of strategies of the opposite sex. This assumes that strategies are uniformly distributed. In other evolutionary games it has been shown that introducing a spatial dimension changes the outcome of the game. In a spatial game, the success of a strategy depends on the location. In a spatial version of the Battle of the Sexes it can be shown that the equilibrium that is present in the non-spatial game does not necessarily emerge when individuals only interact locally. A simulation also shows that the population oscillates around an equilibrium which was predicted when the non-spatial model was first coined and which was previously illustrated using a system of ordinary differential equations.



---

---

## **Acknowledgements**

Many thanks to my supervisor dr. Michael Wilkinson for his time and input. I also would like to thank my second supervisor dr. Henk Bekker. Furthermore, I want to say thanks to all the SAK residents who have provided me with a stimulating work environment during my research.



---

---

# Contents

<b>1</b>	<b>Introduction</b>	<b>1</b>
<b>2</b>	<b>Sexual Conflict</b>	<b>5</b>
2.1	Natural Selection . . . . .	5
2.2	Parental Investment . . . . .	6
2.3	Female Coyness . . . . .	7
2.4	A Game of Conflict . . . . .	8
<b>3</b>	<b>Game Theory</b>	<b>9</b>
3.1	Games . . . . .	9
3.2	Payoff . . . . .	11
3.3	Pure and Mixed Strategies . . . . .	11
3.4	Expected Payoff . . . . .	12
3.5	Minimax Theorem . . . . .	12
3.6	Nash Equilibrium and ESS . . . . .	13
3.7	Asymmetric Games . . . . .	14
3.8	Game Theory in Evolutionary Biology . . . . .	16
3.8.1	Fisher's Principle . . . . .	17
3.8.2	Conflict of Fighting Animals . . . . .	17
<b>4</b>	<b>Battle of the Sexes</b>	<b>19</b>
4.1	Classical Model . . . . .	19
4.2	The Deceitful Male . . . . .	21
4.3	Time Delays . . . . .	23
4.4	Levels of Coyness . . . . .	23
4.5	Mate Selection . . . . .	24
<b>5</b>	<b>Spatial Evolutionary Games</b>	<b>27</b>
5.1	Game of Life . . . . .	27
5.2	Other Spatial Games . . . . .	29

<b>6 Spatial Battle of the Sexes</b>	<b>31</b>
6.1 Cellular Automaton Model . . . . .	31
6.1.1 The Model . . . . .	33
6.1.2 Simulation . . . . .	34
6.1.3 Stable Structures . . . . .	37
6.1.4 Mutations . . . . .	38
6.1.5 Survival of Offspring . . . . .	40
6.2 Partial Differential Equations . . . . .	45
6.2.1 Ordinary Differential Equations . . . . .	45
6.2.2 Diffusion . . . . .	46
<b>7 Discussion</b>	<b>49</b>
7.1 Future Work . . . . .	50
<b>8 Conclusion</b>	<b>51</b>
<b>Bibliography</b>	<b>53</b>
<b>A Equilibrium Derivation</b>	<b>57</b>
<b>B Coordination between the Sexes</b>	<b>61</b>





# Introduction

The sexual reproduction of animals has always been a topic of huge interest to many people, scientists included. The wide variety of behaviour displayed by different species in nature make the act of mating one of the most studied research topics in the field of biology. One of the goals of these studies is not only to record the behaviour but also to make sense of the behaviour. Why do animals behave the way they do? How did their behaviour evolve?

The reproductive process is one of the major sources of conflict in the animal kingdom. In almost all species, males compete with each other to gain the privilege of mating with a female. This competition can take many forms, from physical combat to see which male is the strongest, to a sing-off to determine which male has the most beautiful song. But competition between males is not the only conflict in reproduction. After a male and female mate and their offspring is born, they can have a conflict of interest over who should raise their offspring. Raising offspring requires parents to invest time and assets in their children at their own expense. Both parents would like to minimise their effort, while still having the benefit of having successful offspring. This means both parents will try to get their partner to invest more in the upbringing of their children.

Since the 1970s, evolutionary biology started incorporating game theory in their research. Game theory is a mathematical way of modelling conflict or cooperation between agents. Game theory started out as the study of board games such as chess, but it later proved useful in other fields of science such as economy to model real-life situations.

In evolutionary biology, games can be used to model conflict such as fights between animals of the same species. It has been observed in nature that animals hold back in fights when fighting their own species. A game-theoretical model can give insight into the conflict and show why the limited war fighting strategy that is observed is the most stable strategy from an evolutionary standpoint. Other models are used to explain the existence of female coyness, a mating strategy which is present in many different species of animals.

Coy females require a male partner to invest an extended period of time in their relationship before mating and having offspring together. One could argue that this period of courtship is not beneficial for the female, since the time she invests in the relationship lowers her reproductive output. Natural selection favours genes that maximise their reproductive output. Thus, in a world of natural selection, how could a supposedly inferior coy strategy survive?

It has been suggested that females are coy in order to secure the assistance of their male partner. In 1976, Dawkins [8] addressed the existence of female coyness in his book *The Selfish Gene*. He modelled mate selection as a game of conflict which he referred to as the *Battle of the Sexes*. This very basic mathematical model shows that female coyness can survive given the presence of two male strategies, males that are helpful in raising offspring and males that are unhelpful. Though this model shows how female coyness could be evolutionary stable, it is a very abstract version of reality. Many efforts have been made since to make the model more realistic [19, 21, 35, 38].

One of the aspects in mate selection that the classical model does not take into account is the spatial aspect of animal mating. In the real world, an individual can only interact – or mate – with other individuals that are spatially close to them. Most game theoretical models that try to explain female coyness do not address the spatial aspect of a game. It could very well be that introducing a spatial aspect to the Battle of the Sexes changes the outcome of the game.

The spatial aspect of games has been studied for various games using computer simulations where large populations of individuals interact with each other. These simulations show results that are different from their non-spatial versions for some games. This includes classic game theoretical games such as Hawks vs. Doves [15] and Prisoner's Dilemma [26, 28, 29]. In these spatial games, some strategies benefit from the spatial structure and perform much better than in the non-

spatial game.

The research presented in this thesis is aimed at expanding the existing model of the Battle of the Sexes to include a spatial dimension. The goal is to determine what the effect is of adding a spatial dimension to this game.

This thesis has the following structure. First the sexual conflict between parents that is observed in nature is introduced, followed by a short introduction of the most important concepts in game theory. Dawkins game-theoretical model of the conflict and its extensions are discussed in chapter 4. After a short background of spatial evolutionary games, the Battle of the Sexes is modelled as a spatial game by means of a cellular automaton. An alternative model using a set of partial differential equations is also discussed and compared to the cellular automaton model. The last two chapters are reserved for discussion and conclusion.



# Sexual Conflict

In many species of animals there is a conflict between a male and female who mate. Females will benefit if they can get the help of their partner in raising their offspring. For males, helping to raise the offspring comes at the cost of being able to have more offspring. Many biologists believe that the female can secure the male's assistance by being coy. A coy female requires a potential mate to engage in a period of courtship. If a male is willing to invest in the relationship before mating he is more likely to invest in the offspring after it is born.

## 2.1 Natural Selection

Natural selection favours genes that are most successful in reproducing. The idea of natural selection was introduced by Darwin in his *On the Origin of Species* [6] in 1859 and still forms one of the cornerstones in modern biology.

Genes are important to living organisms. They carry the information to build and maintain the cells of an organism, which can be referred to as the genotype of an organism. The genotype of an organism is important in determining the phenotype of the organism. The phenotype is the observable traits that an organism possesses.

Genetic information is passed on by means of reproduction. Genes that are passed on more than others will become more numerous and spread throughout the gene pool. A successful phenotype spreads its genotype. This way, a gene can survive over time until another gene proves more successful.

For many animals, reproduction is achieved when a male and a female mate and have offspring together. Both parents pass part of their genes onto their offspring. The best strategy to copy genes is to have a lot of offspring. However, this does not necessarily mean that those genes will survive over time. If an individual has a lot of offspring that dies before that offspring is able to reproduce, the reproductive output of that individual will essentially be zero. For parents, it is important that their children survive long enough to have children of their own. The parents can increase the life expectancy of the offspring by providing care. Parental care can be defined as the investment of assets from a parent's own life to its offspring. For example, feeding or guarding can increase the offspring's chance of surviving (and hence their reproductive success) [37].

Although caring for your offspring may seem like an altruistic act, it has been suggested that it born out of "selfish" motives. The parent is concerned with the survival of its own genes. Dawkins [8] even argued that the behaviour of an animal might be driven by their genes and that behaviour is encoded in the genes. A view which is shared by many other biologists. It means that parents pass both their genes and their behaviour onto their children. This way natural selection also favours behaviour that is most successful at reproducing.

## 2.2 Parental Investment

When a male and a female have offspring together they have a mutual interest in raising it. Though there are exceptions, in most cases both parents share a large part of their genes with their offspring. Raising this offspring requires parents to invest in their young. This investment comes at a cost. Time or assets that have been invested in one child could have been invested alternatively. This means that parents will want to limit their *parental investment*.

The most fair way for a couple to raise offspring is if both parents equally care for their young. However, a parent that can get its partner to invest more than its equal share will eventually be better off. A parent that spends less time raising offspring has more time to invest in new offspring and will increase its reproductive output. This is where a conflict arises between the parents who both want to minimise their effort and who both want their partner to invest more than their fair

share.

There is a fundamental difference between males and females in reproduction. For a male, the number of children he can have is not limited by the number of sex cells he can produce, but by his ability to fertilise eggs with those cells. A female is much more limited in the number of children she can have, she is limited by the number of eggs she can produce [37]. This means that the female has a larger minimal parental investment than the male. Even at the point of conception, the female – whose sex cells are larger – has invested more in her offspring than the male.

In most animals, the parent that is most likely to leave first is the male. In mammals for example, the female carries the offspring after mating. If the male leaves before the offspring is born, the female will have to raise it by herself. If she leaves too, her offspring will most likely not survive and all her effort will be lost<sup>1</sup>. The female will benefit if she can get her partner to stay and help out in caring for the offspring. In evolutionary biology, it is suggested that a female can secure the male's help with an *engagement period* (or *courtship period*). A male has to invest a period of time in the relationship. During this period the female has the opportunity to inspect the male. If the male is likely to help out in raising the offspring, the female can proceed with their relationship. If the male is likely to desert her after mating, she can reject him in order to find a more helpful mate. This way the female lowers the risk of getting involved with an unfaithful male and carrying the burden of raising offspring alone.

## 2.3 Female Coyness

When a couple meets for the first time, the male is usually fertile and ready to mate immediately while the female requires a period of male presence before she is willing or able to start reproducing [2, 38]. Only after the male has invested time or assets in their relationship will the female be open for reproduction together. This female behaviour is referred to as female *coyness* or female *choosiness*.

---

<sup>1</sup>An important note on past parental investment versus future parental investment is raised by Dawkins & Carlisle [9]. Parents will prefer offspring that requires a minimum amount of investment in the future. In this case a potential new child would need more investment to reach adulthood than one which has already been born.

A study in pigeons shows that the ovaries of a female can enlarge more than fourfold during the physical presence of a male [2]. This means that the female is ready to reproduce after a male has invested effort – in this case time – in the relationship. Time is one of the best ways for a female to assess a male's commitment. A resourceful male could persuade multiple females into mating by presenting them with gifts, but he can only be physically with one female at a time. Time is a limited resource for every male. This is especially true for animals that have mating seasons. Most species – humans being a notable exception – have a short period each year in which to secure a partner for reproduction.

## 2.4 A Game of Conflict

The period of courtship that precedes mating is not only costly for a male, who is unable to find new partners during the period, but it is also costly for the female who invests precious time. Simply put, all the time the female wastes during courtship she could have invested in having offspring. So why does the female impose a period of courtship upon a male when it does not seem beneficial for either herself or her partner?

The conflict of interest between males and females has been named the *Battle of the Sexes* by Dawkins [8]. He introduced a game theoretical approach to explaining how female coyness could have evolved and why coy behaviour is evolutionary stable. In his model both males and females adopt one of two strategies. Females can be either *coy* or *fast* and males can be either *helpful* or *unhelpful* (which Dawkins calls *faithful* and *philandering* respectively). Each strategy has its own corresponding behaviour. A coy female requires a male to invest in the relationship before mating. A fast female does not require a male to invest in the relationship. A helpful male will invest in a relationship and will help raise the offspring when it is born. An unhelpful male is not willing to enter an engagement period and will not help out with raising offspring.

Using this game theoretical approach it can be shown that, although it does not always seem beneficial for a female to be coy, coy behaviour can survive through evolution if some conditions are met.

# Game Theory

Game theory concerns the modelling of strategic decision making. It is a mathematical study of models that describe conflict or cooperation between rational agents. The first theorems in game theory addressed board games such as chess [32, 39]. It was later shown that games can be a useful model for real-life situations.

Games as studied in the field of game theory have a some characteristics. A game is played by multiple “players”, each of which adopts a certain “strategy” in order to “win”. These terms are all very abstract and they apply in very different situations, especially when the game models real-life situations. For example, in the financial world competing companies (players) have a certain corporate plan (strategy) to maximise their profit (win). This is quite different from a cactus (a player) which grows spines (a defence strategy) in order to survive (win).

Today, game theory is applied in economics [4, 13, 25], political science [20], sociology [5], psychology [3, 12], biology [5] and many other fields of science. Many scientists see game theory as a useful tool to gain insight into complex problems.

## 3.1 Games

One of the most important aspects of a game are the rules. The rules of a game give a player a number of options to play the game. These options are often described as strategies in the context of game theory. A multi-player game consists of a set of players which can choose from

a set of strategies and it is assumed that all players try to “win” the game.

Games can be subdivided into two groups: games with full information and games without full information. In a game of full – or complete – information, every aspect of the game is known to all players. Examples of such games are chess or *tic-tac-toe*. Each time a player has to take a decision every possible outcome can be determined. This can be displayed in a decision tree. Even though a player does not know in advance what the next move of their opponent will be, a player can assume that their opponent will play the best move possible. For a simple game as *tic-tac-toe* this means that an experienced player never has to lose. When two of such players meet the game will always end in a draw.

In games where there is no full information some aspects of the game are hidden to the players. In a card game such as poker for example, cards are dealt randomly and a player has to guess what cards their opponent may have. In this case it is harder to adopt a winning strategy.

Chess, *tic-tac-toe* and poker are all games where players play sequentially. In many of the games addressed in game theory the players do not play sequentially, but simultaneously, in which case the game is always without full information.

A simple example of such a game is *Rock, Paper, Scissors*. In this game, two players simultaneously choose one of three objects: rock, paper or scissors. Each object can beat one other object. Scissors can cut paper, paper covers rock and rock breaks scissors. The winner of the game is the player that chooses an object that can beat the object of its opponent. If both players pick the same object the game ends in a draw. So if player *A* chooses rock and player *B* chooses scissors, player *A* wins and player *B* loses.

Because the players chose simultaneously the players lack the knowledge to pick the winning strategy. However, it may still be possible to play a strategy that is “best”. In the games that will be considered in the remainder of this thesis are all simultaneous games.

## 3.2 Payoff

When players win a game there is something to be earned. To denote the benefit that players receive given the strategies they play a payoff matrix can be used. In the payoff both the benefit and the cost of the competition are considered. In a game where player  $A$  plays against player  $B$ , the rows of the payoff matrix are the strategies that player  $A$  can choose and the columns are the strategies that player  $B$  can choose. The values in the matrix are the payoff for player  $A$ .

For a game of Rock, Paper, Scissors the payoff matrix is given in table 3.1. If player  $A$  chooses Rock and player  $B$  chooses Paper, the payoff for player  $A$  is -1. The payoff for player  $B$  in this case is 1.

In this game the sum of the benefit of player  $A$  and player  $B$  is always zero. Any game where the sum of the benefit of all players is always zero is called a *zero-sum game*.

## 3.3 Pure and Mixed Strategies

A player which always adopts the same strategy in a game is said to have a *pure strategy*. Players with a pure strategy play games deterministically, which means that a game which has the same initial conditions will also have the same outcome. If a player has a *mixed strategy*, the player chooses a pure strategy with a certain probability.

In the example of Rock, Paper, Scissors a pure strategy would be a player that always chooses the same object. A player with a mixed strategy varies the choice of their object randomly according to some distribution.

	Rock	Paper	Scissors
Rock	0	-1	1
Paper	1	0	-1
Scissors	-1	1	0

Table 3.1: The payoff matrix for a game of Rock, Paper, Scissors.

### 3.4 Expected Payoff

In many games, players belong to a population. Within a population, players with different strategies can be present. More often than not, players do not know which strategy they will encounter in advance. If it is known advance which strategy a player will encounter, it would be easy to pick a good strategy when playing against a player with a pure strategy. If your opponent always plays Rock, you play always Paper.

For a player with a mixed strategy, this is not so easy. However, if there is a known distribution of strategies there is a certain probability of encountering any strategy. Given the payoff matrix and the probability of playing against any strategy, the expected payoff  $P$  of a game can be calculated (equation 3.1).

$$P(S) = \sum_T p(T)E(S, T) \quad (3.1)$$

In this equation  $p(T)$  is the probability of encountering a player with strategy  $T$ ,  $E(S, T)$  is the payoff that a player with strategy  $S$  receives when it plays against a player with strategy  $T$ .

In a game of Rock, Paper, Scissors, an opponent that is unbiased will pick any strategy with the probability  $\frac{1}{3}$ . Thus, the expected payoff of playing the strategy Rock against this player is:

$$\begin{aligned} P(R) &= p(R)E(R, R) + p(P)E(R, P) + p(S)E(R, S) \\ P(R) &= \frac{1}{3} \cdot 0 + \frac{1}{3} \cdot -1 + \frac{1}{3} \cdot 1 \\ P(R) &= 0 \end{aligned}$$

The same holds for Paper and Scissors. This means that no matter which strategy a player picks, when playing against a player with an unbiased mixed strategy the expected payoff is always 0.

### 3.5 Minimax Theorem

One of the foundations of game theory is the *minimax theorem*. This theorem was proved by John von Neumann in 1928 [24]. It describes a two-player zero-sum game with finite pure strategies in which both players try to minimise their maximum loss.

**Theorem.** *For every two-person, zero-sum game with finitely many strategies, there exists a value  $V$  and a mixed strategy for each player, such that (a) Given player 2's strategy, the best payoff possible for player 1 is  $V$ , and (b) Given player 1's strategy, the best payoff possible for player 2 is  $-V$ .*

Minimax is a decision rule that minimises the maximum loss for a player.

### 3.6 Nash Equilibrium and ESS

In games with multiple players, a state in which no player can improve its profit by changing its strategy is called an *equilibrium point* [22, 23], which has been named the *Nash equilibrium*. This state is often seen as a “solution” of a game theoretical problem. If the game reaches such a point, the players will not change their strategy. For zero-sum games the minimax solution is a Nash equilibrium.

**Theorem.** *Let  $E(S, T)$  represent the payoff of playing strategy  $S$  against strategy  $T$ . The strategy pair  $(S, S)$  is a Nash equilibrium in a two-player game if and only if the following holds for every strategy  $T \neq S$ :  $E(S, S) \geq E(T, S)$ . If  $E(S, S) > E(T, S)$  for all  $T \neq S$ , then  $(S, S)$  is a strict Nash equilibrium.*

Rational players will only change their strategy if it pays to do so. If a game is at a Nash equilibrium no player will change their strategy, thus the game stays in the same state. A refinement of the Nash equilibrium by Selten [33] is the *trembling hand equilibrium*. This equilibrium considers a player that may play an unintended strategy with a small probability. This unintended play may cause the system to “jump out” of a Nash equilibrium. An equilibrium that can withstand such a play and return to the equilibrium is called a trembling hand equilibrium. A trembling hand equilibrium is more robust than a Nash equilibrium.

There are more refinements of the Nash equilibrium, the main goal of which is to reduce the number of “solutions” of a game and to make those solutions more robust. In many games there are equilibria that are very unlikely to occur.

A Nash equilibrium and a trembling hand equilibrium are both related to an *Evolutionary Stable Strategy* (ess), which was introduced

by Maynard Smith [17, 18]. An evolutionary stable strategy is a strategy which, if it is adopted by an entire population can not be invaded by any strategy that is initially rare. This means that the strategy performs better against itself than any other strategy or it is equally good against itself than any other strategy, but better against that strategy than it is against itself. Only pure strategies can be an ess.

**Theorem.** A strategy  $S$  is an ess if  $E(S, S) > E(T, S) \vee (E(S, S) = E(T, S) \wedge E(S, T) > E(T, T))$  for all  $T \neq S$ .

### 3.7 Asymmetric Games

In some games, two players may have different roles and different corresponding interests. This means that the payoff matrix of the players is different. These games are called *bimatrix games* or *asymmetric games*.

A good example of asymmetry in games can be illustrated with a game of conflict known as *Hawks vs. Doves*, which is generally symmetric but has an asymmetric extension. Hawks vs. Doves is a game that was introduced to describe animal behaviour. It models two birds who have a conflict over a resource, such as food. Each bird can be either a hawk – who is aggressive – or a dove who is not aggressive. If two hawks meet, they fight over the food until one of them is injured and withdraws. In this case one bird gains food, while the other has the cost of being injured. If a hawk meets a dove, the dove flees at the first sign of aggression. The dove gains nor loses anything, while the hawk gains the food. If two doves, meet they share the food and both gain half of the food.

Suppose the food has a value of  $V$  and being injured comes at a cost, say  $C$ . If two hawks meet they fight until one of them is injured. If they have a 50/50 chance of winning, their expected gain is  $V/2 - C/2$ . A full

	Hawk	Dove
Hawk	$V/2 - C/2$	$V$
Dove	$0$	$V/2$

Table 3.2: The payoff matrix for a game of Hawks vs. Doves.  $V$  denotes the value of the resource and  $C$  denotes the cost of being injured.

payoff matrix is given in table 3.2. It is usually assumed that  $V < C$ . This inequality together with the payoff matrix forms the *extensive form* of the game, a concept first described by von Neumann [24].

From this payoff matrix the equilibrium can be derived. At an equilibrium, the payoff  $P$  of both strategies should be equal. The payoff for a strategy depends on the probability of meeting each strategy  $p(D)$  and  $p(H)$  ( $D$  for dove and  $H$  for hawk).

$$\begin{aligned} P(D) &= P(H) \\ (V/2)p(D) &= (V/2 - C/2)p(H) + Vp(D) \\ -(V/2)p(D) &= (V/2 - C/2)p(H) \end{aligned}$$

Since  $p(D) + p(H) = 1$ , the equilibrium can be expressed in terms of the probability of meeting one of the strategies.

$$\begin{aligned} -(V/2)p(D) &= (V/2 - C/2)p(H) \\ -(V/2)(1 - p(H)) &= (V/2 - C/2)p(H) \\ -(V/2) + (V/2)p(H) &= (V/2 - C/2)p(H) \\ -(V/2) &= -(C/2)p(H) \\ V/C &= p(H) \end{aligned}$$

Thoes that the probability of meeting a hawk at the equilibrium is equal to the ratio between the value food and the cost of injury. Suppose  $V = 4$  and  $C = 8$ . At the equilibrium, half of the population is a hawk and half of the population is a dove, and both strategies have an expected payoff of 1.

When a population is large a change of strategy by an individual does not influence the frequency of hawks  $p(H)$  (or the frequency of doves  $p(D)$ , which is related to the frequency of hawks  $p(D) = 1 - p(H)$ ). This means that no individual can improve its payoff by switching. However, in this case there is no penalty for individual for switching, which means that none of the strategies can be an ess. If more individuals switch strategies the ratio can change. When this happens one strategy will have a slight advantage over the other and the ratio will move back to the equilibrium. This process can repeat itself which means that the ratio will oscillate around the equilibrium. A population in which the

		Intruder	
		Hawk	Dove
Owner	Hawk	$((V + K)/2 - C/2, V/2 - C/2)$	$(V + K, 0)$
	Dove	$(0, V)$	$((V + K)/2, V/2)$

Table 3.3: The payoff matrix for the asymmetric version of Hawks vs. Doves. The each cell contains two values, the first is the payoff for the owner, the second for the intruder.  $K$  denotes the additional value of the resource to the owner.

genetic composition is restored after a small disturbance is said to be in an *evolutionary stable state* [17].

The game changes if one of the two birds is the owner of the resource while the other is an intruder trying to steal the resource. This can happen when food is in the territory of one of the birds. The food can be more valuable to the owner since he has invested in acquiring it in the past. In this case the roles are different and there are two different payoff matrices: one for the owner and one for the intruder (see table 3.3). The additional value to the owner is indicated with  $K$ .

In this asymmetric game, an owner always plays against an intruder. This means that the payoff of an owner depends on the ratio of strategies of intruders, and vice versa. Suppose  $K = 4$ , now hawk and dove perform equally well if the intruder is a hawk, both gain 0. If the intruder is a dove, the hawk performs better. This means that it is better to be a hawk if you are the owner. For intruders, nothing has changed. However, over time all owners will have adopted a hawk strategy. In that case it is better to be a dove when intruding.

### 3.8 Game Theory in Evolutionary Biology

Game theory has been adopted by many fields of science as a useful way to model real-life situations. In evolutionary biology, game theory and evolutionary game theory in particular has led to many new models of animal behaviour. The conflict between parents over parental investment that described in chapter 4 is just one example of a game theoretical model that is used in evolutionary biology. Often these models show how a particular behaviour can prove itself evolutionary stable even though this is not clear at first sight.

### 3.8.1 Fisher's Principle

The use of game theoretic arguments in evolutionary biology goes back to 1871 when Charles Darwin described how natural selection equalises the sex ratio [7]. This was later formalised by Fisher in the 1930s [10]. It is now known as *Fisher's principle*.

A 1:1 sex ratio does not seem like the best strategy to produce a lot of offspring since one male can mate with many females. In an artificial environment, such as a farm, the 1:1 ratio almost never exists. A farmer has few males that inseminate many females to maximise the output. For a farmer, an extra male means investing in more food, more space and more attention while the gain is minimal. So why does this strategy not survive in nature?

Suppose there is a population of a certain species where the females far outnumber the males. This means that a newborn male has better mating prospects than a newborn female. Consequently, he will produce more offspring and his genes will become more numerous in the gene pool. This means that parents who have a tendency to produce males will have a greater number of grandchildren. If this tendency is genetically determined, the number of males in the population will increase. As soon the ratio approaches 1:1 the advantage of producing more male offspring fades away. Since the same reasoning holds for female offspring, the 1:1 ratio is an equilibrium.

When the ratio is 1:1, any individual that produces offspring with a different ratio will shift the population slightly away from the 1:1 ratio, which slightly lowers the chances for its offspring to reproduce.

### 3.8.2 Conflict of Fighting Animals

In the 1970s, Maynard Smith [16, 18] used game theory to analyse the conflict between fighting animals. When animals of the same species fight they often adopt a "limited war" strategy. This essentially means that they hold back and do not try to cause serious injury to their opponent. In many species of snakes, fighting males do not use their fangs, but wrestle each other until one of them wins. This behaviour has often been explained as the result of group selection, which means the behaviour benefits the group as a whole and not the individual. The game theoretical model by Maynard Smith shows that there is a gain for an individual as well.

This model is a variation to the previous described Hawks vs. Doves game with more strategies included. The different strategies considered by Maynard Smith show that for many animals it is better to hold back and only be aggressive when provoked than to be aggressive all the time. Animals who are aggressive all the time cause each other a lot of injury, it is therefore better to be peaceful. However, a population of only peaceful animals can get overrun by aggressive animals. The strategy of only being aggressive when provoked prevents the population to be invaded by aggressive animals while having the benefit of being peaceful when aggressive animals are not around.

# Battle of the Sexes

A game-theoretical model that describes sexual conflict can help form an understanding of why the interaction between males and females in mate selection evolved the way it did. The first model of this game was formalised by Dawkins in the 1970s. This game is known as of the Battle of the Sexes.

## 4.1 Classical Model

Dawkins [8] explains the existence of female coyness by modelling the interactions between males and females as a bimatrix game. Each sex adopts one of two strategies which are caricatures of natural behaviour. Males can be either strictly helpful or unhelpful, females can be strictly coy or fast.

The game is played as follows. A male and a female meet and based on both their strategies they act a certain way and receive a certain payoff. When a fast female meets a male partner, they mate immediately. After mating, if the male is helpful he will help the female raise the offspring and the two parents share the cost of upbringing equally. If the male is unhelpful, he leaves after mating and the female has to raise the offspring by herself. When a coy female meets a male partner she insists that the male engages into a period of courtship first. If the male is unhelpful he refuses to do so and leaves. A helpful male will engage in a courtship period after which the couple mates and raises the offspring together.

To calculate the payoff that the male and female receive the following actions should be quantified: the benefit of having offspring, which will be denoted with  $G$ , the cost of raising offspring,  $C$ , and the cost of being involved in an engagement period,  $E$ .

- If a fast female and a helpful male meet both gain  $G$ . They share  $C$ , so both have a cost of  $\frac{C}{2}$ . Both parents receive a payoff of  $G - \frac{C}{2}$ .
- If a fast female and an unhelpful male meet both gain  $G$ . The male has no costs, thus his payoff is  $G$ . The female has to raise the offspring alone which costs her  $C$ . Her payoff is  $G - C$ .
- If a coy female and a helpful male meet both gain  $G$ . First they both have a cost  $E$ , which is the cost of engaging in a period of courtship. They share the cost of upbringing. The payoff for both parents is  $G - E - \frac{C}{2}$ .
- If a coy female and an unhelpful male meet they do not mate. Both have a payoff of 0.

It is very hard to find a good measure for the gain of having offspring or any of the other actions. Dawkins assigns arbitrary values to the benefit of having offspring, the cost of upbringing and the cost of an engagement period, namely  $G = 15$ ,  $C = 20$  and  $E = 3$  respectively. The payoffs that follow from these values are given in table 4.1. With the values, the success of a male strategy can be expressed as a function of  $v$ , the frequency of coy females. The same can be done for female strategies, that are a function of the frequency of helpful males  $u$ . With these functions a value for  $v$  can be determined for which both male strategies are equally successful. By doing the same for the female strategies, the equilibrium for the system can be determined. For the values proposed by Dawkins the system is in equilibrium when the frequency of helpful males  $u^* = \frac{5}{8}$  and the frequency of coy females  $v^* = \frac{5}{6}$  (see appendix A for the entire derivation).

	Coy	Fast
Helpful	(2, 2)	(5, 5)
Unhelpful	(0, 0)	(15, -5)

Table 4.1: The payoff matrix for the Battle of the Sexes, using the values proposed by Dawkins:  $G = 15$ ,  $C = 20$ ,  $E = 3$ .

Dawkins stated that this mixed equilibrium was an evolutionary stable strategy. However, the equilibrium does not satisfy one of the conditions for an ESS [21, 31]. In general, in asymmetric games only pure strategies can be an ESS as was proved by Selten [34]. This means there is no ESS in this game, just an equilibrium of mixed strategies.

## 4.2 The Deceitful Male

The classical model contains two strategies for each sex. In nature however, there is nothing that prevents a new strategy from emerging. Suppose an unhelpful male tries to trick coy females into mating with him. This new strategy will be called *deceitful male*. In the presence of a fast female a deceitful male acts just like an unhelpful male. In the presence of a coy female the deceitful male acts like a helpful male at first. He engages in a period of courtship. The female will think the male is helpful and after their courtship the couple mates. The deceitful male then leaves the female to care for her young alone just like he would with a fast female.

In other research, all helpful are considered to be deceitful [19, 38]. It has not yet been illustrated how this strategy holds up against the traditional male strategies in the Battle of the Sexes.

This new strategy can be included in the payoff matrix (table 4.2). From this matrix we can see that a deceitful male performs better than a helpful male for every interaction. He can successfully mate with every female he meets without ever have to pay the cost of upbringing. This would mean that helpful males would disappear when a deceitful male enters the population.

A deceitful male also performs better than an unhelpful male. In a population of only fast females they perform just as well, but for every coy female in the population a deceitful male performs better than an

	Coy	Fast
Helpful	(2, 2)	(5, 5)
Unhelpful	(0, 0)	(15, -5)
Deceitful	(12, -8)	(15, -5)

Table 4.2: Payoff matrix for the Battle of the Sexes with the deceitful male included. Values used are  $C = 20$ ,  $G = 15$ ,  $E = 3$ .

unhelpful one. Whether or not unhelpful males go extinct depends on coy females. If coy females go extinct before unhelpful males all males will essentially behave the same and perform equally well. It is likely that coy females will go extinct when helpful males have disappeared. Without helpful males a coy female only will mate with a deceitful male. In this case she is always worse off than a fast female, no matter who the fast female mates with.

With this current set of strategies there is nothing that can stop the rise of the deceitful male. However, if males can adopt a new strategy, there is no reason why females could not do the same thing. A third female strategy could be the *perceptive female*. A perceptive female is a coy female but one with the skill to detect whether or not a male is deceitful. If the perceptive female is in a period of courtship with a deceitful male she can discover his intentions. She will refuse to mate with the male. Both will lose  $E$ , but the female does not have to raise offspring alone (see table 4.3).

Against this new female strategy the deceitful male performs worse than both original male strategies. This means that in the presence of perceptive females helpful and unhelpful males will not go extinct. The original coy female will perform worse than the perceptive female when there are still deceitful males around. The original coy female will disappear and when she does, so will the deceitful male.

The population will then be back to two strategies per sex, with the same payoff matrix as before. Switching to nature one can conclude that the male skill of being deceitful is not evolutionary stable when females can develop the skill of being perceptive.

	Coy	Fast	Perceptive
Helpful	(2, 2)	(5, 5)	(2, 2)
Unhelpful	(0, 0)	(15, -5)	(0, 0)
Deceitful	(12, -8)	(15, -5)	(-3, -3)

Table 4.3: Payoff matrix for the Battle of the Sexes with the perceptive female included. Values used are  $C = 20$ ,  $G = 15$ ,  $E = 3$ .

### 4.3 Time Delays

One of the drawbacks of the model by Dawkins is that time is not modelled explicitly. The payoff that is derived in this model is the payoff per interaction. To analyse the reproductive output of an individual it may be more useful to look at the payoff per unit of time. There is a big difference in the time spent on a specific interaction. The interaction between a coy female and an unhelpful male will typically be short. The interaction between a fast female and an unhelpful male will be short for the male, but long for the female who has to raise the offspring.

These time differences can be modelled explicitly. Mylius [21] shows a model for a population of animals where the payoff matrices are replaced by time delays in which individuals can not find a new mate. In this model, individuals can be free, paired or single parent. The free individuals have one of the four strategies from the original model and it is assumed they mix homogeneously through the population. Paired individuals are either courting or raising their offspring. There are three possible types of couples: a courting helpful male and coy female, a raising helpful male and coy female, a raising helpful male and fast female. A single parent is either a fast female or widow(er), since Mylius includes mortality in his model.

In the model, male offspring inherits the strategy of its father and female offspring inherits the strategy of its mother. This makes the inheritance of genetics more explicit than in the classical Battle of the Sexes. The model simulates the evolution of the population. The results show that the existence of female coyness depends on various conditions.

### 4.4 Levels of Coyness

In the classical model coyness is binary. A female can be either coy or not and all coy females adopt the same engagement period. One could say that all females are equally coy. Dawkins uses these caricatures for a reason. He is interested in showing that coyness can survive in evolution. In reality, females will have a certain level of coyness. The perceptive female that was presented in section 4.2 will need a certain amount of time to inspect a male before she knows his intentions. The more time she invests, the more she learns about the male and the

smaller the probability will be that she makes a mistake. But the longer she waits with her decision, the smaller the chance that she will find a suitable alternative partner during the current mating period.

McNamara et al. have created a model which predicts the optimal level of female coyness [19]. In this model the males are either helpful or unhelpful. During the engagement period a female tries to learn the male's intentions. If this engagement period is too short there is a big risk of picking an unhelpful male, but if the engagement period is too long the female wastes valuable time. This scenario is slightly more realistic than the original Battle of the Sexes where females know a male's intentions directly when they interact.

In the model females can have a certain level of coyness. This means that the length of the courtship period varies. The optimal length of a courtship period is determined by the number of males in a population and the ratios between male strategies.

The model by McNamara et al. focuses on females. Males are still strictly unhelpful or helpful. Like females, it is unlikely that males will behave this absolute in nature. A male can leave at any point in time. Like coyness, helpfulness can come in different levels. This is might be a good next step to take with this model.

## 4.5 Mate Selection

Courtship may have more advantages to females than just securing a male's help. During a period of courtship an individual has a partner, but still has an opportunity to switch. A female can reject her partner if she finds a better and available partner. Of course, this is not just the case for females, but for males as well. Switching is not always a good strategy. For example, if the courtship period with one partner is almost completed – the investment in the relationship is high – switching partners may be very costly as a new period of courtship begins in which there is no reproduction.

This process has been captured in a model by Simão & Todd [35]. The model has a focus on human mate selection, but it may also provide insight on animal mate selection in general. Although the model doesn't focus on female coyness, it does address some interesting aspects of mate selection.

In the model all individuals have a list of potential mates. Every

single individual looks for the best potential mate. During courtship, both males and females still keep their eye out for a better partner. Females may abort a courtship period not because a male is not faithful or helpful, but because another partner can potentially give her “better” offspring.



# Spatial Evolutionary Games

Evolutionary games have been an important method developing models in evolutionary biology. In evolutionary games a population plays a game repeatedly. Through selection based on the success of individuals the population changes or evolves.

In spatial evolutionary games, the location of the players in the population plays a role in their success. The players have local interactions to determine their success. A great example of a spatial evolutionary game is Conway's Game of Life, but other evolutionary games can be played in a similar way.

## 5.1 Game of Life

In the 1970s, Conway developed a cellular automaton that is since been known as *Conway's Game of Life* or sometimes *Life* for short [11]. The game is played on an infinite two-dimensional space. The space is divided in square cells each of which can be either "dead" or "alive". Each cell interacts with its direct neighbours in the following way:

- Any living cell that has less than two living neighbours dies because of under-population.
- Any living cell that has two or three living neighbours survives and will live in the next generation.
- Any living cell that has more than three living neighbours dies because of over-population.

- Any dead cell that has exactly three living neighbours is brought to life in the next generation.

The game starts with an initial population and then evolves according to the rules. These rules are carefully chosen to prevent explosive growth or fast extinction. An example of the evolution of a game is given in figure 5.1 where the first five generations of a game are displayed. It is important to note that the state of any cell in the next

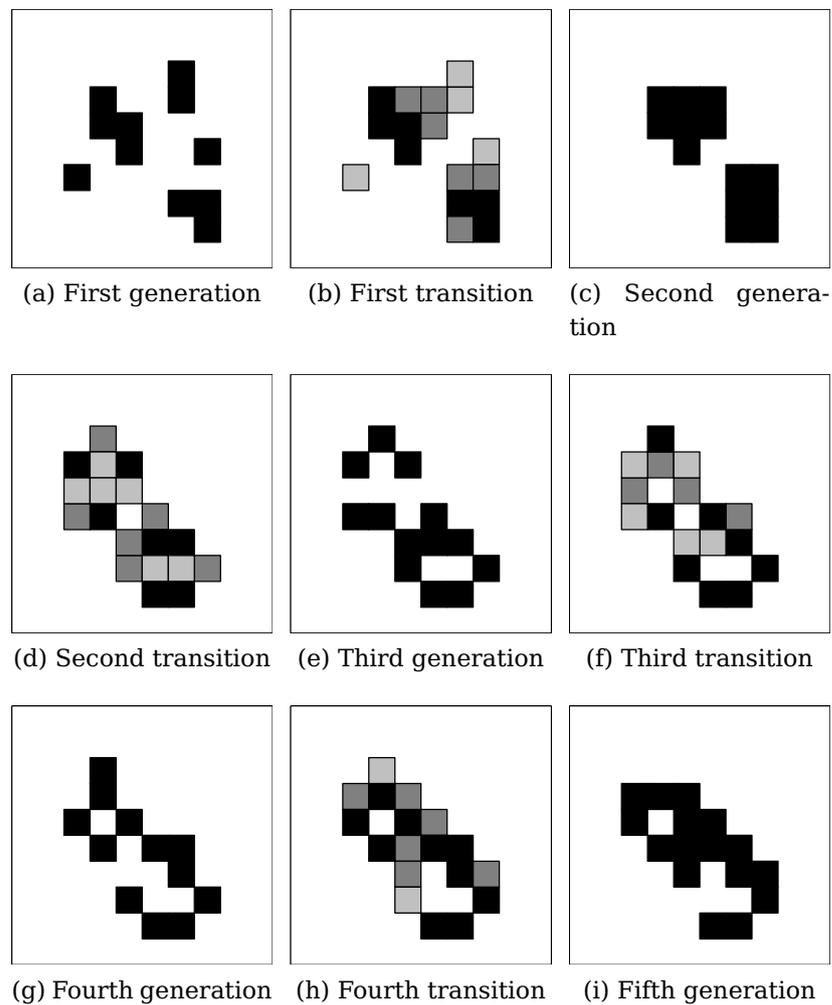


Figure 5.1: An example of the evolution of Conway's Game of Life. Living cells are black, dead cells are grey, living cells that die in the next generation are light grey, dead cells that are brought to life in the next generation are dark grey.

generation only depends on its own current state and the state of its eight neighbours.

One of the most fascinating aspects of Conway's Game of Life is that one can construct different patterns. These patterns include still patterns, oscillators and moving oscillators. A still pattern is a set of cells that does not change between generations. This means that each living cell has two or three neighbours and that no dead cell has three or more neighbours. An oscillator is a pattern that changes between generations but after a number of generations is in the same state as a previous generation. From this generation onwards it will cycle in exactly the same way. A moving oscillator is different from an oscillator in that way that after a number of generation returns to the same pattern as a previous generation only shifted in space.

## 5.2 Other Spatial Games

Research on multi-player games has led to spatial versions of the Ultimatum Game [30], the coordination game [35], the Prisoner's Dilemma [26, 27, 28] and Hawks vs. Doves [15].

The both the classic version and the asymmetric version of Hawks vs. Doves have been explained in section 3.7. Another extension to this game is to add a spatial component. The game can be played on a two-dimensional space that is divided into cells, just like Conway's Game of Life. Instead of being dead or alive, the cells are now one of the two strategies: hawk or dove. Each cell interacts with each of its neighbours by playing the game against each other. The cell then looks at its own total payoff and compares it to the payoff of their neighbours. If one of the neighbours is doing better, the cell changes their strategy to the strategy of this neighbour.

In the spatial model the strategies form clusters. A dove that is surrounded by other doves will do pretty well. Since he performs quite well his neighbours will adopt that strategy in the next population. This means that the dove that is surrounded by doves will also be surrounded by doves in the next round. The spatial structure really benefits doves in a cluster of doves.

The game Hawks vs. Doves knows another extension where two new strategies are introduced, a retaliator and a bully. When the additional strategy of the retaliator is included in the spatial model the emerging

clusters have a big effect on the number of hawks in the population. In a spatial version, hawks are worse off than in the classical game due to spatial pattern formation [15]. The outcome of the game is changed significantly. The retaliator, which is seen as a cooperating strategy, benefits from cluster formation.

Nowak & May [26, 27, 28] describe spatial Prisoner's Dilemma. This game shows results similar to spatial Hawks vs. Doves, with cooperators performing better in a spatial structure.

The classic Prisoner's Dilemma describes a situation where two cooperating criminals are arrested. The police offers both criminals a deal. If a criminal cooperates and testifies against their partner while the partner stays silent, the criminal is set free and their partner receives a heavy sentence. If both remain silent, they both receive a short sentence. If both testify, they both receive a medium sentence. Both criminals have to make their decision in isolation, without knowing what their partner does.

The spatial model used by Nowak & May shows interesting pattern formation. Like Conway's Game of Life, each cell has its own strategy and their strategy in the next generation is determined by the number of neighbours they have with a certain strategy. In this game however, the rules allow strategies to cluster, while Conway's Game of Life was specifically designed to prevent this. The model can be expanded beyond the original grid for example by using a grid with more dimensions or a grid where cells are randomly distributed.

# Spatial Battle of the Sexes

Like Hawks vs. Doves and the Prisoner's Dilemma, the Battle of Sexes can also be played in a spatial manner. The research of spatial versions of Hawks vs. Doves, Prisoner's Dilemma and other spatial games shows that the outcome of a spatial game can be quite different from the regular game. If this is the case for these games, it could very well also be true for the Battle of the Sexes.

In spatial evolutionary game theory a strategy changes if other strategies that are spatial close to them are performing better. This corresponds to the evolution in nature where successful phenotypes replace the less successful phenotypes.

## 6.1 Cellular Automaton Model

A general definition of a spatial evolutionary game is given by Killingback & Doebeli [15]. They consider a game with a finite set of strategies. They use a finite number of cells arranged in a lattice which represents space, which can be any dimension. Every cell is occupied by one strategy. Each cell has a set of neighbouring cells. In each iteration, for each cell the sum of payoffs of playing against each of their neighbouring cells is determined. This sum is the total payoff and it is used to determine the strategy of the cell in the next iteration. The highest total payoff amongst a cell and its neighbours determines the strategy of the cell in the next generation. A model constructed in this way is a finite cellular automaton.

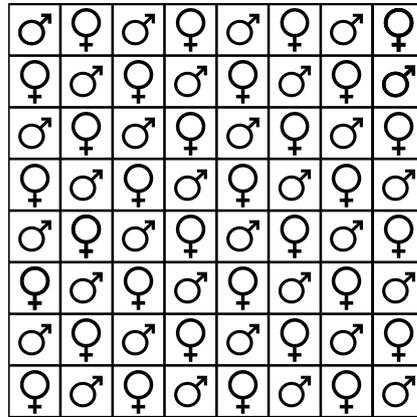


Figure 6.1: Placement of males and females in a chessboard fashion on a two-dimensional square grid. Using periodic boundary conditions each cell has eight neighbours: four male and four female.

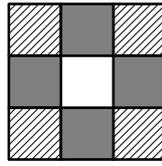


Figure 6.2: The neighbours of a cell (white) in a cellular automaton for a bimatrix game. The “mates” of the cell are grey, the “competitors” of the cell are hatched.

Alonso-Sanz [1] describes a model of the spatial version of a coordination game<sup>1</sup> which is a variation of the general model given by Killingback & Doebeli. Since the coordination game is an asymmetric game a slight adaption is needed. In the model players are placed on a two-dimensional grid. Males and females are placed in a chessboard fashion as illustrated in figure 6.1. Using periodic boundary conditions each cell has eight neighbours, four male and four female.

In each iteration a player determines its payoff by playing against each neighbour of the other sex (their mates, see figure 6.2). After each player has determined its total payoff it adopts the strategy of the neighbour of the same sex that has the highest payoff (the strategy that

<sup>1</sup>This coordination game is referred to by Alonso-Sanz as the Battle of the Sexes, though the game is somewhat different from the game of sexual conflict that was described by Dawkins. This is illustrated in appendix B.

is locally the best). The general definition of Killingback & Doebeli mentions the possibility of letting cells interact with themselves. However, since a coordination game is an asymmetric game self-interactions are not defined.

As the Battle of the Sexes is also a game played by players of two types, this model can be used as a basis for a spatial version of the Battle of the Sexes.

### 6.1.1 The Model

Using the cellular automaton described above, a population can be simulated. The population plays the Battle of the Sexes as follows:

1. Initialise the population
2. Calculate the payoff for each player
3. Update the strategy for each player
4. Repeat from 2

First, a population is initialised with parameters  $N$ ,  $u_0$ ,  $v_0$ . The size of the grid is  $N \times N$ , so there are  $N^2$  cells. Each cell is inhabited by one strategy and male and female strategies are placed in an alternating fashion. This means there are  $\frac{N \times N}{2}$  males and  $\frac{N \times N}{2}$  females in the population<sup>2</sup>. To keep the periodic boundary conditions intact  $N$  should be an even number. The values  $u$  and  $v$  are the frequencies of helpful males and coy females in the initial population ( $0 \leq u \leq 1$  and  $0 \leq v \leq 1$ ). Since there are two strategies per sex, the frequency of unhelpful males is  $1 - u$  (and  $1 - v$  for fast females). When  $u = 0$  there are no helpful males in the population and when  $u = 1$  there are no unhelpful males in the population. The population initialised with each male having a chance of  $u_0$  of being helpful (and unhelpful otherwise), each female has a chance of  $v_0$  of being coy (and fast otherwise).

In each time step the total payoff for each cell is calculated, which is the sum of the payoff of one interaction with each of its four mates. To calculate this payoff same values are used as for the regular Battle of the Sexes (see table 6.1).

---

<sup>2</sup>The equal ratio between the sexes is based on both observations in nature and Fisher's principle.

	Coy	Fast
Helpful	(2, 2)	(5, 5)
Unhelpful	(0, 0)	(15, -5)

Table 6.1: The payoff matrix for the Battle of the Sexes, using the values proposed by Dawkins:  $G = 15$ ,  $C = 20$ ,  $E = 3$ .

After the payoff of all players is calculated for the current time step, each player updates its own strategy. Each player adopts the strategy which is the most successful among their competitors and themselves. In some cases it is necessary to define a tie-breaking rule to decide which strategy a player will adopt when two different strategies in the neighbourhood have the same payoff. For example, using the payoff matrix with the values proposed by Dawkins it is possible for a female to have one coy competitor with a payoff of 0 (she has four unhelpful mates) and one fast competitor with a payoff of 0 (two unhelpful mates and two helpful mates). In this model, the tie-breaking rule will be deterministic, where there is a set order used to chose a strategy. This deterministic tie-breaking rule makes the whole model deterministic.

The strategy of a cell in the next time step is influenced by 17 cells, the cell itself, its mates, its competitors and the mates of its competitors. This means that the neighbourhood is larger than for most symmetric spatial games where the neighbourhood is of size 8 or 9.

### 6.1.2 Simulation

A visualisation of a simulation is shown in figure 6.3 where a population is displayed with different colours for different strategies. The simulation is initialised ( $t = 0$ ) with an equal ratio in strategies. In each time step the population changes. The random pattern of strategies quickly disappear and is replaced by clusters of the same strategy.

To illustrate the effect of a spatial dimension a simulation is done with a population of  $500 \times 500$ . The population is initialised with  $u_0 = 0.5$  and  $v_0 = 0.5$ . This means that there are about 62 500 individuals of each strategy present at the start of the simulation ( $t = 0$ ). Figure 6.4 shows how the ratio of strategies in the population changes in the first 50 time steps.

The strategies unhelpful and fast go (nearly) extinct rapidly. The population then stabilises. Repeating the simulation with the same ini-

tial values (but with the initial population distributed in a different way) gives the same results, meaning that the same strategies are dominant after some time.

The final – stable – population depends on the ratio of strategies in the initial population. Especially the initial value for female coyness

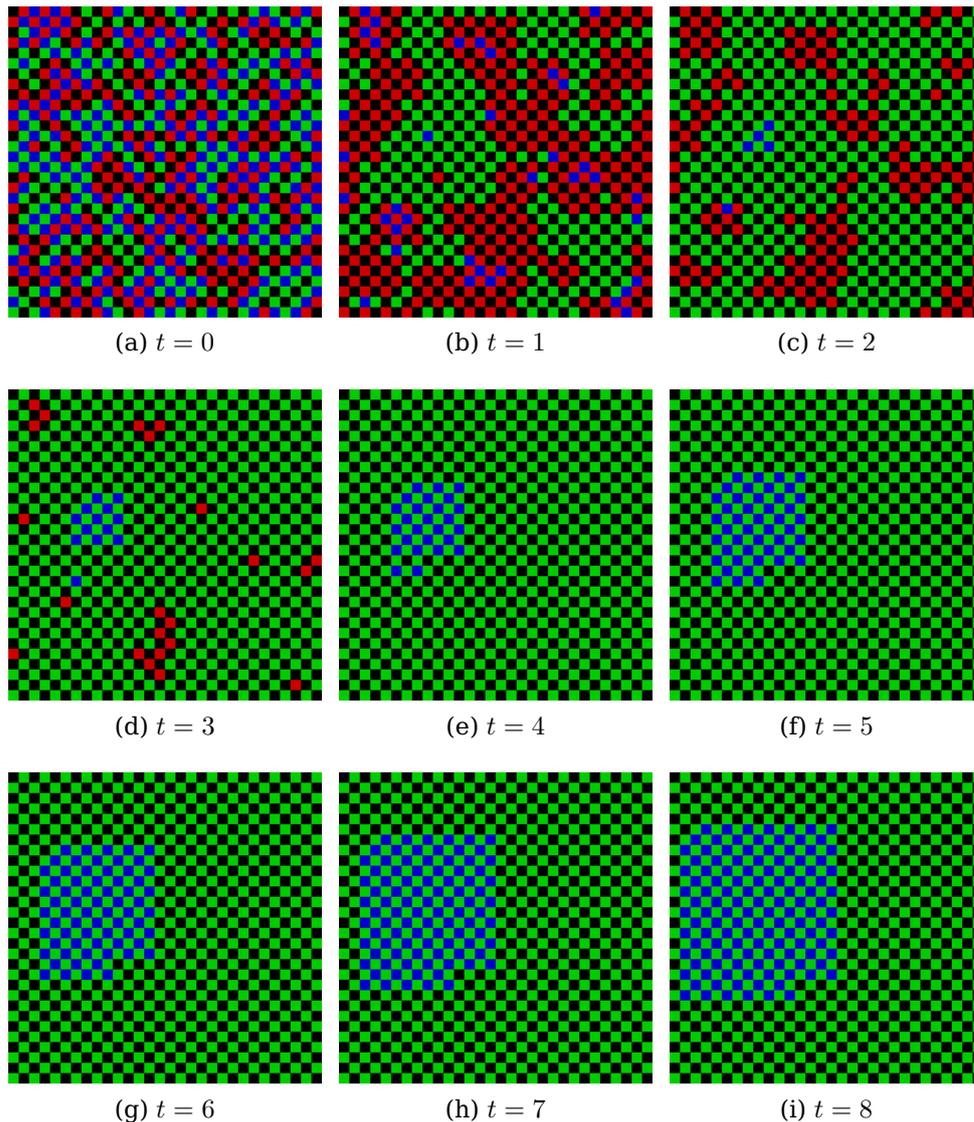


Figure 6.3: Visualisation of a simulation of a  $30 \times 30$  population playing the Battle of the Sexes in a cellular automaton. Strategies are colour coded: red for fast females, green for coy females, blue for helpful males and black for unhelpful males.

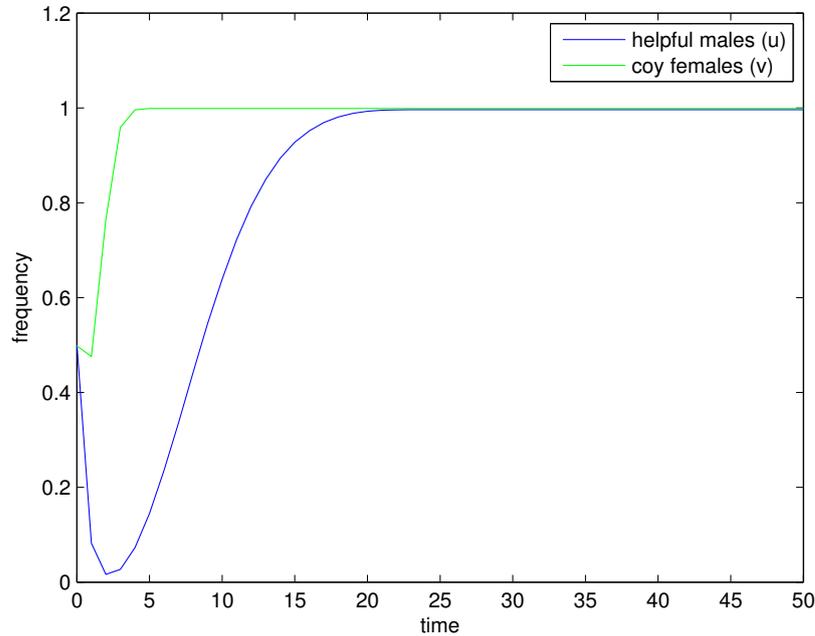


Figure 6.4: The change of strategies in a population ( $500 \times 500$ ) through time for a simulation of the Battle of the Sexes with a cellular automaton. Using Dawkins's payoff matrix and initial values  $u_0 = 0.5$  and  $v_0 = 0.5$ .

( $v_0$ ) influences the outcome of the simulation. Coy female behaviour will always emerge as the only female strategy unless there are no coy females or no unhelpful males to begin with. Which male strategy emerges depends on the initial female coyness. When coy females are initially rare (e.g.  $v_0 = 0.1$ ), all males will eventually be unhelpful. In the case where coy females are common in the initial population, all males will eventually be helpful. Table 6.2 shows the resulting stable populations for different initial values  $u_0$  and  $v_0$ . In the cases where  $u_0$  or  $v_0$  is 0 or 1 a strategy is missing from the initial population and thus will not be present in the final population.

The situation where the final population is exists of only coy females and unhelpful males is unrealistic in nature. Since coy females and unhelpful males refuse to mate together, no offspring will be born. This situation is the result of few coy females in the initial population. With many fast females around, the unhelpful males outcompete the helpful

Initial condition	$v_0 = 0.0$	$v_0 = 0.1$	$v_0 = 0.5$	$v_0 = 0.9$	$v_0 = 1.0$
$u_0 = 0.0$	F/U	C/U	C/U	C/U	C/U
$u_0 = 0.1$	F/U	C/U	C/H	C/H	C/H
$u_0 = 0.5$	F/U	C/U	C/H	C/H	C/H
$u_0 = 0.9$	F/U	C/U	C/H	C/H	C/H
$u_0 = 1.0$	F/H	F/H	F/H	F/H	C/H

Table 6.2: Strategies present in a stable (final) population for different initial values of  $u$  and  $v$ . Population size is  $500 \times 500$ . C stand for coy females, F for fast females, H for helpful males and U for unhelpful males.

males to the point where helpful males go extinct. When unhelpful males are extinct, the fast females are outcompeted by the coy females until the female population exists out of only coy females.

In every scenario, two dominant strategies emerges and form a stable population. This is quite different from the equilibrium that follows from the non-spatial Battle of the Sexes.

### 6.1.3 Stable Structures

For some initialisations the strategies unhelpful and fast go extinct completely. For other initialisations a small number of individuals with these strategies survive and the number of individuals with those strategies stay stable over time. This is the result of “stable structures” that can emerge. A stable structure moves through the population but it does not change shape. This is similar to the moving oscillators in Conway’s Game of Life, except that their shape does not change, it only moves over the lattice. Figure 6.5 shows examples of these stable structures.

Similar structures are also addressed by Nowak & May [26, 28, 29] for spatial versions of symmetric games. These structures will never disappear. When the model reaches such a state it could be argued that it is not an equilibrium. For a number of players it pays to switch their strategy which is what causes the movement of the structure. In the context of the spatial evolutionary games it is usual to look at change of the ratio of strategies to determine if a system is at an equilibrium point. Even though the individual players still change their strategy, the ratio of strategies is stable and will stay stable forever.

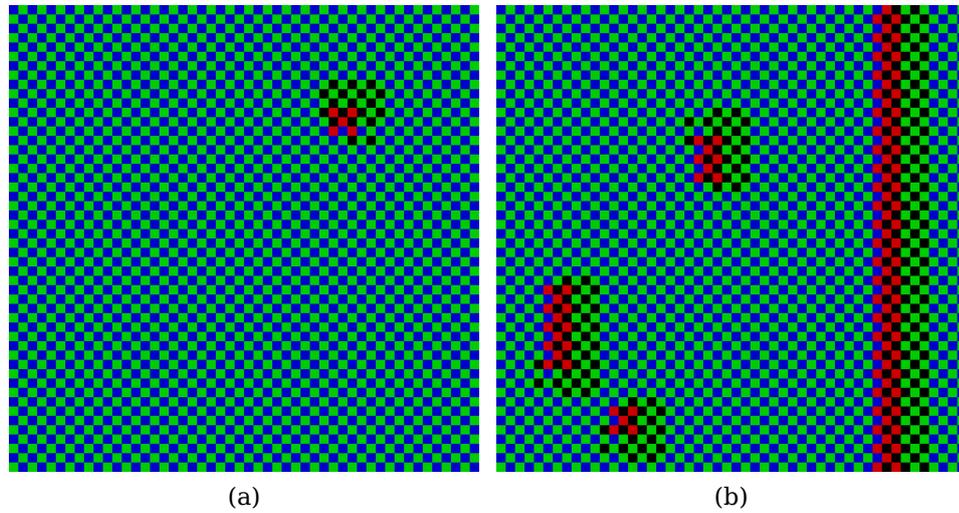


Figure 6.5: Examples of populations with a structure of strategies which stays stable over time.

#### 6.1.4 Mutations

One of the requirements for strategies in a population to be evolutionary stable is that they can not be invaded by another strategy. A population of only helpful males and coy females can be invaded by a “mutant” easily. In the context of this model, a mutant is a female that changes her strategy from coy to fast without having a good reason to do so. This mutation will prove very beneficial in the current population. The fast female has the advantage of not investing in an engagement period. Since all males are helpful, there is no need to check if a male is helpful or not during an engagement period.

Mutations can and should be included in the model. A mutation is implemented as a player that changes its strategy stochastically. To show the effect that mutations can have on the model a mutation parameter  $m$  is included. Figure 6.6 shows a simulation with the same parameters as figure 6.4 but with a mutation occurring at a rate of one mutation per 1000 strategy updates ( $m = 0.001$ ).

With mutations, no strategy will go extinct, instead the ratio between strategies oscillates. This oscillating effect was predicted by Dawkins and worked out by Schuster and Sigmund [31] for his model. The inclusion of mutations shows that the populations that emerge in the spatial model without mutations are not an ess.

In the spatial model the strategy ratios do not oscillate around the equilibrium that was suggested by Dawkins. Instead, the strategy ratios oscillate around a different point (figure 6.7). Especially the frequency of female coyness is lower than what could be expected from the non-spatial model. This suggests that fast females benefit from a spatial structure.

In the spatial model, bigger populations have smaller amplitude of the oscillations. This is illustrated in figure 6.8. Though the amplitude of the oscillation is different, the average is very similar. The size of a population does not effect the equilibrium of the spatial model.

There is a question of how often mutations should occur. In general, if mutations are rare it gives populations of pure strategies the chance to grow before they are invaded. This means that it takes longer for a system to go back to the equilibrium. The rate of mutations has an effect on the amplitude of the oscillations.

The rate of mutations also has an effect on the equilibrium of the

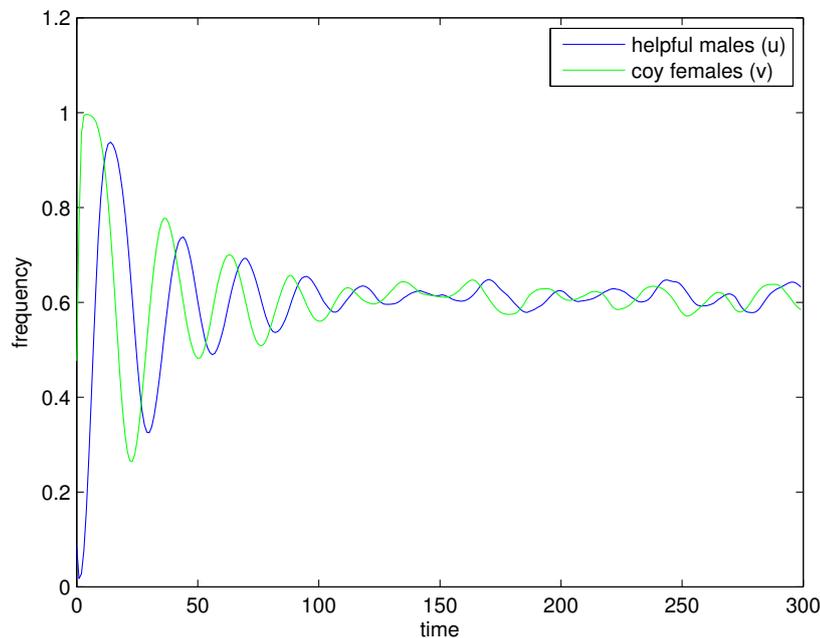


Figure 6.6: The strategy ratios in a population when mutations occur ( $m = 0.001$ ). The other settings are the same as for the simulation in figure 6.4.

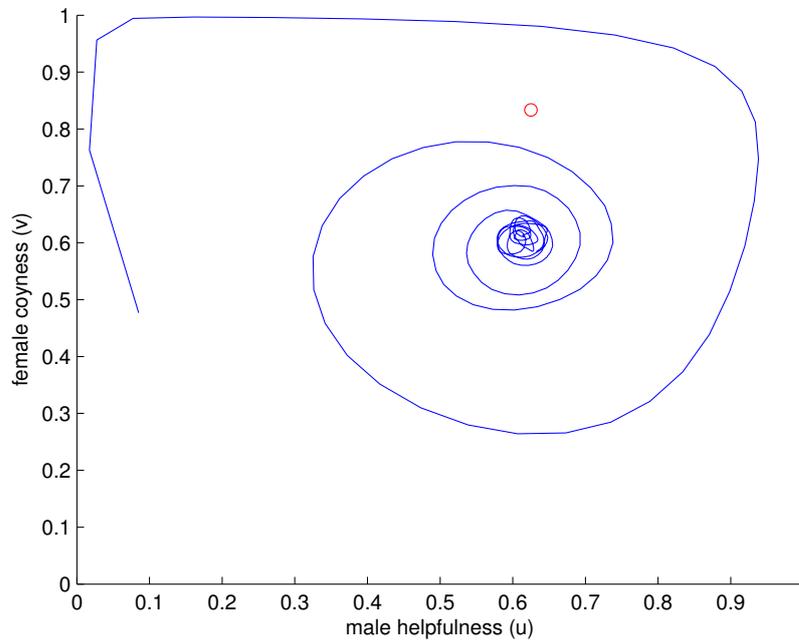


Figure 6.7: The evolution of strategy ratios towards an equilibrium. This figure corresponds to figure 6.6. The equilibrium  $(u^*, v^*)$  of the non-spatial game is marked with  $\circ$ .

system itself. For example when mutations are very common ( $m = 0.1$ ) the system shows a quite different equilibrium (figure 6.9a) than when mutations are not common (for example  $m = 0.0001$  in figure 6.9c). Common mutations benefit male unhelpfulness and female coyness.

### 6.1.5 Survival of Offspring

The reproductive output of a parent highly depends on the survival rate of their offspring. Offspring that dies before having children of their own does not benefit the reproductive output of its parent. In most cases, the expected survival rate of offspring that is raised by two parents is higher than the expected survival rate of offspring raised by a single parent. In the case of two parents, if one parent dies the other can still raise the offspring. In the case of a single parent, if it dies the offspring is left alone and has a lower chance of surviving. In other words, the gain for raising offspring together should be higher than the

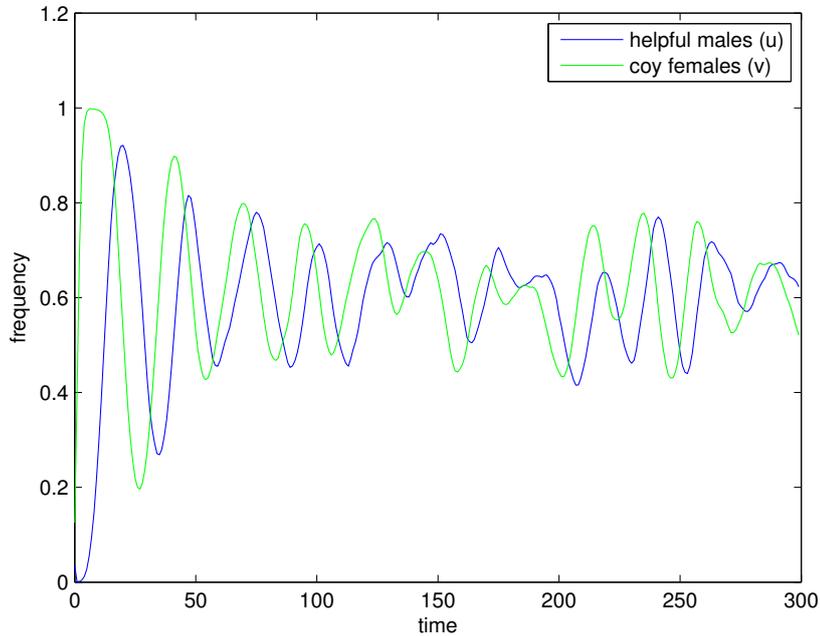


Figure 6.8: The amplitude of the oscillations around the average depends on size of a population. Larger populations such as in figure 6.6 have smaller amplitudes than a smaller population displayed here (10 000 individuals). All other settings are the same.

gain for raising offspring alone.

The effect of this difference can be determined by introducing  $G_1$  and  $G_2$ , the gain of raising offspring alone or raising offspring together respectively, with  $G_1 < G_2$ . When a male deserts a female the survival rate of their offspring (and thus the reproductive output of the parents) drops. Both parents gain  $G_1$ . If parents raise their offspring together they gain  $G_2$ . This idea is present in the model of Mylius [21] where the reproductive output of parents who share the cost of upbringing is

	Coy	Fast
Helpful	(2, 2)	(5, 5)
Unhelpful	(0, 0)	(3, -17)

Table 6.3: The payoff matrix for the Battle of the Sexes where the gain of having offspring raised by a single parent is reduced,  $G_1 = 3$ .

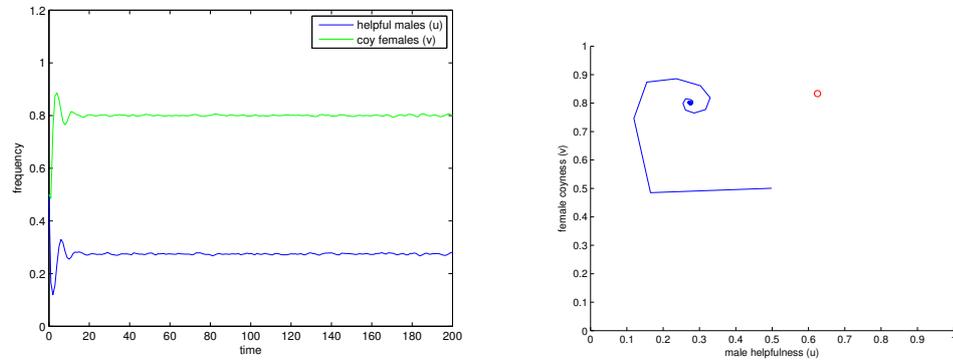
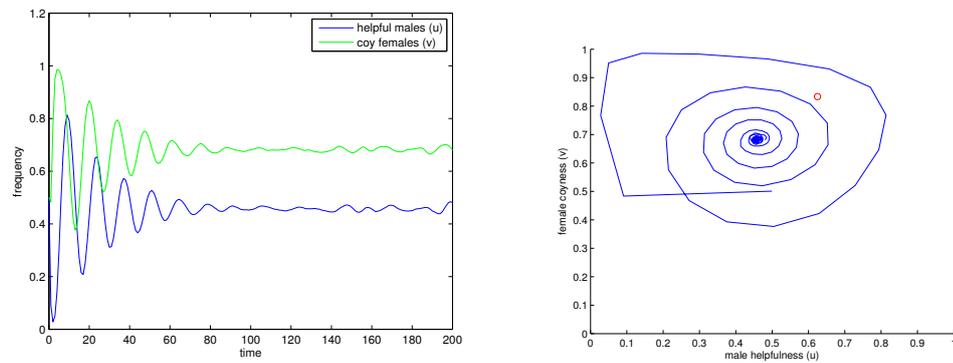
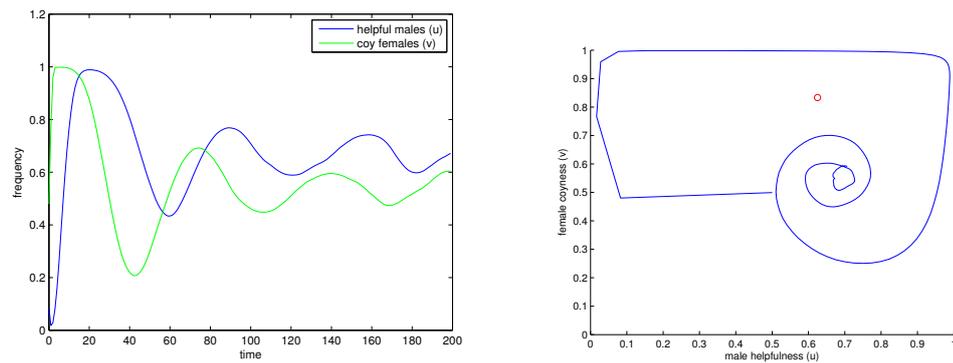
(a) Mutation rate  $m = 0.1$ (b) Mutation rate  $m = 0.01$ (c) Mutation rate  $m = 0.0001$ 

Figure 6.9: The effect of mutation rate on the evolution of the strategy ratios. Settings are the same as in figure 6.6. The classic equilibrium  $(u^*, v^*)$  is marked with  $\circ$ .

higher than that of a single parent. The model also accounts for one of the parents dieing.

Within different species the benefit for raising offspring together as opposed by raising it alone can be very different. Children in species that have to worry about predators may need more guarding by the parents than the young of the predator. Mylius models this with a parameter  $k$  which is close to 1 for species where raising offspring together hardly pays off and  $k$  is small for species where the advantage of raising offspring together is great. This parameter corresponds to the ratio  $G_1:G_2$ .

Mylius states that female coyness and male helpfulness will not be able to survive  $k$  is close to 1. If  $k$  is small, it does not pay for males to be unhelpful and only helpful males survive. In that case, it does not pay for females to be coy since all males will share the cost of upbringing anyway. Suppose  $G_1$  is 3 and  $G_2$  is 15 (see table 6.3). The helpful male now performs better than the unhelpful male in every interaction.

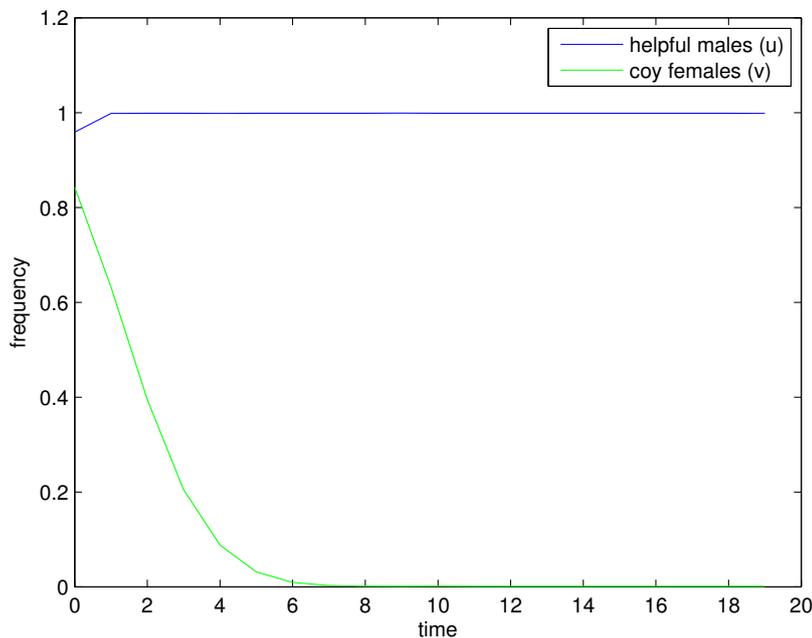


Figure 6.10: The ratio between strategies when the gain between raising offspring together is greater than raising offspring alone. Here, parents of offspring raised by a single parent only gain  $G_1 = 3$ .

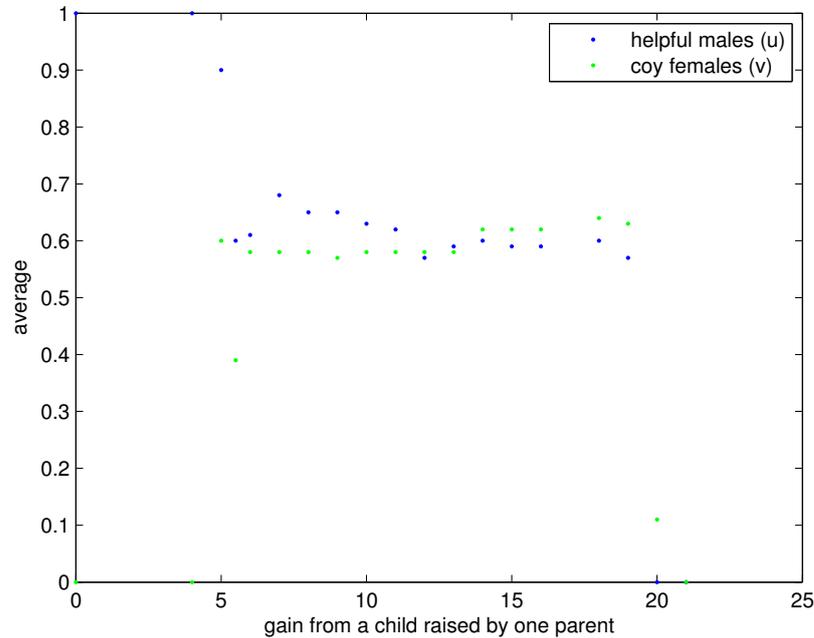


Figure 6.11: The average ratio between strategies when the gain between raising offspring together is different than raising offspring alone over an extended period of time.

A simulation shows that using this payoff matrix only the strategies of the helpful male and the fast female are evolutionary stable (figure 6.10) even when mutations are present. In this case a strategies of helpful males and fast females are an ess.

Varying  $G_1$  can show different outcomes (figure 6.11). For  $G_1 < 5$  the population consists of fast females and helpful males. This is in fact an ess, the population can not be invaded by either coy females or unhelpful males. For  $5 < G_1 < 20$  the population is mixed with all four strategies present. The ratios in this range of  $G_1$  are fairly stable, with male helpfulness around  $\frac{6}{10}$  and female coyness around  $\frac{6}{10}$ . When  $G_1 > 20$  there emerges an ess of unhelpful males and fast females.

The critical points of  $G_1 < 5$  and  $G_1 > 20$  are not surprising. With these values the extensive form of the payoff matrix changes.

## 6.2 Partial Differential Equations

To illustrate the instability of the mixed equilibrium found in the classical Battle of the Sexes a dynamic system can be constructed. This can illustrate the oscillating effect that was predicted by Dawkins. The use of ordinary differential equations to model the dynamics of games was introduced by Taylor & Jonker [36, 21].

From this set of ordinary differential equations, partial differential equations can be derived which can describe a system with a spatial dimension.

### 6.2.1 Ordinary Differential Equations

The frequency of coy females and helpful males is a value that changes through time. Schuster & Sigmund [31] derived ordinary differential equations that describe the system using Dawkins payoff matrix. The success of helpful males depends on the frequency of coy females. This

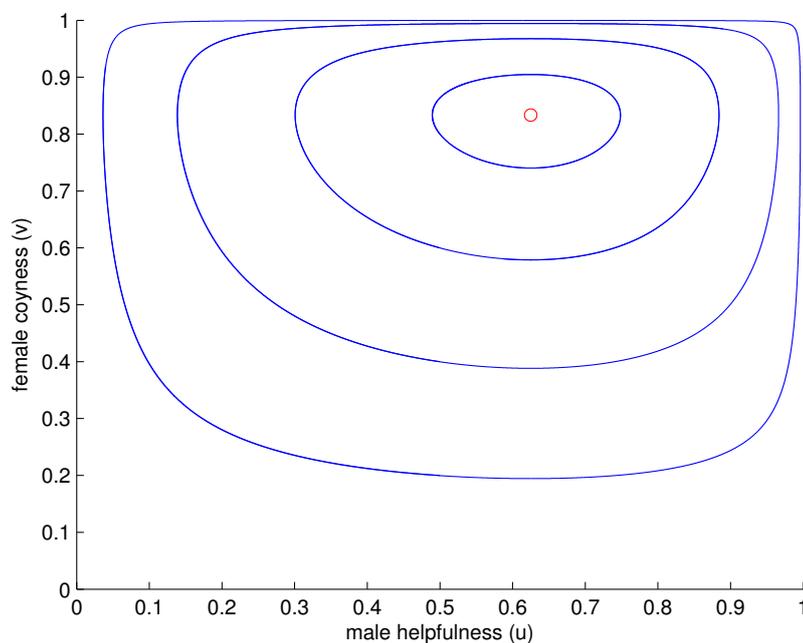


Figure 6.12: Dynamic analysis of a population using ordinary differential equations. The equilibrium  $(u^*, v^*)$  is marked with  $\circ$ .

means that the frequency of helpful males in the future depends on the frequency of coy females in the present.

$$\begin{aligned}\dot{u} &= u(1-u)(-10+12v) \\ \dot{v} &= v(1-v)(5-8u)\end{aligned}\tag{6.1}$$

Here,  $u$  is the frequency of helpful males and  $v$  is the frequency of coy females ( $0 \leq u \leq 1$  and  $0 \leq v \leq 1$ ).

They concluded that the solutions of this ordinary differential equation (ODE) system are neutrally stable oscillations around the mixed equilibrium point  $(u^*, v^*)$  [21]. Figure 6.12 shows the behaviour of the system for four different initial values of  $(u, v)$ . The value of  $u_0$  and  $v_0$  determines the amplitude of the oscillation.

The time average which can be determined with Dawkins model corresponds with the measurements done by biologists, which concentrates on the percentage of males that is helpful over time rather than viewing an evolutionary stable state [31].

### 6.2.2 Diffusion

To include the spatial aspect in this approach one can use a partial differential equation (PDE). In this case, the spatial approach has two dimensions. The frequency of helpful males (and the other strategies) now also depends on a location  $(x, y)$ .

In nature, populations may not be well mixed. Animals are mobile and this results in transport. One way of modelling transport is diffusion. Suppose there is a two-dimensional grid with 1000 animals at each location  $(x, y)$ . Each time step 100 of the animals at a location travel to four neighbouring regions, 25 in each direction. Each location loses 100 animals and receives 100 animals in return from neighbouring regions.

If  $u$  and  $v$  at a location  $(x, y)$  are different from the  $u$  and  $v$  at the neighbouring regions, the transport of animals will effect this  $u$  and  $v$ .

In the two dimensional case this diffusion can be defined as:

$$\begin{aligned}\frac{\partial X}{\partial t} &= D \left( \frac{\partial^2 X}{\partial x^2} + \frac{\partial^2 X}{\partial y^2} \right) \\ \frac{\partial X}{\partial t} &= D \nabla^2 X\end{aligned}\tag{6.2}$$

where  $D$  is the diffusion constant and  $\nabla$  is defined as:

$$\nabla = \begin{pmatrix} \frac{\partial}{\partial x} \\ \frac{\partial}{\partial y} \end{pmatrix}$$

The diffusion term (equation 6.2) can be added to the ODE system (equations 6.1) to construct a PDE system.

$$\begin{aligned} \frac{\partial u}{\partial t} &= u(1-u)(-10+12v) + D\nabla^2 u \\ \frac{\partial v}{\partial t} &= v(1-v)(5-8u) + D\nabla^2 v \end{aligned} \quad (6.3)$$

The diffusion can be approximated using a finite difference method.

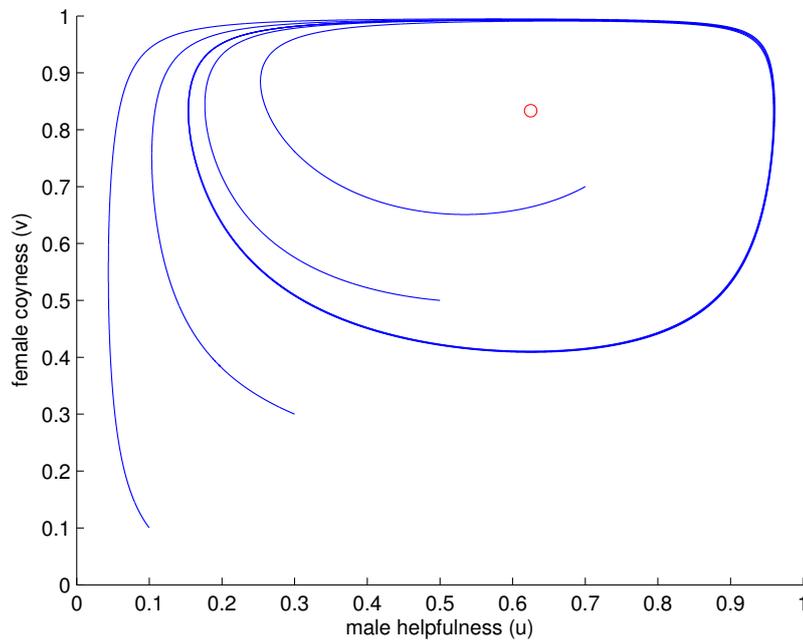


Figure 6.13: Dynamic analysis of a population using partial differential equations. The diffusion constant  $D$  is set to an intermediate level. The equilibrium  $(u^*, v^*)$  is marked with  $\circ$ .

$$\frac{\partial^2 u_i}{\partial x^2} = \frac{u(x_{i+1}, y_i, t) - 2u(x_i, y_i, t) + u(x_{i-1}, y_i, t)}{\Delta x^2} + O(\Delta x^2)$$

$$\frac{\partial^2 u_i}{\partial y^2} = \frac{u(x_i, y_{i+1}, t) - 2u(x_i, y_i, t) + u(x_i, y_{i-1}, t)}{\Delta y^2} + O(\Delta y^2)$$

A population of animals lives in an area. Suppose the animals are uniformly distributed, but their strategies are not. A two-dimensional regular grid is placed over the area. For each cell, the ratio of strategies is determined. For each cell, the ratio of strategies in the next generation now depends on the current ratio of strategies which determines the reproductive success, and the ratio of strategies in the neighbouring cells from which animals will travel to that cell.

The diffusion constant  $D$  determines how many animals will migrate in each time step. If  $D$  is zero, there is no interaction and each cell will behave just like the ODE. For  $D$  is non-zero, neighbouring cells interact. Eventually the diffusion causes the population at each location to become homogenous over time. When the population is homogenous the system behaves just like the ODE system.

In figure 6.13 an area is divided into four cells, each with their own initial strategy ratios. Diffusion allows the population to mix well. Because of this, the spatial aspect loses its influence quickly. A PDE system with diffusion is not a great way to illustrate the effect of uneven distribution of strategies as it will even the distribution within the population.

### Discussion

The Battle of the Sexes has been an influential model in evolutionary biology. Though it has proven itself to be a powerful argument there are some aspects that should be considered.

The Battle of the Sexes focuses only on female coyness. Though for many animal species it is the female who is coy, there are reasons for males to display coy behaviour as well. When a male and female mate soon after their first encounter, the male can not be sure that the offspring that is born is actually his. There is a possibility the female has mated with another male. If the male waits for a period of time and keeps an eye on her he can ensure that any offspring that is born will be his own. This prevents him from raising offspring that is not his own. In this case, the engagement period be beneficial to helpful males.

There are also species where it is the female that has the first opportunity to leave. In many species of fish, the female releases her eggs and the male has to fertilise them. The fertilised eggs do not grow in the females body as is the case for mammals. A female fish has the opportunity to leave as soon as she has released her eggs. In response, a male may refrain from fertilising the eggs, so a female may stick around until her eggs are fertilised. At that point, both parents have an equal opportunity of deserting.

The classical model of the Battle of the Sexes assumes that if one parent leaves, the other parent will invest twice as much in the offspring in order to raise it. This means that for the offspring it doesn't matter whether it is raised by one parent or two. It will always receive the same amount of care. The assumption that the survival rate of off-

spring raised by a single parent is lower than offspring raised by two parents is generally true in nature. As mentioned, this effect highly varies per species of animals. An interesting case of a species where these two assumptions do not hold is the rock sparrow. In rock sparrows, desertion of the offspring can occur in both sexes. When the parents are together, both try to minimise their parental effort. This means that the care that the offspring receives is minimal. If one of the parents leaves, there is no longer a conflict between the parents and the parent that remains no longer has a strong drive to minimise their parental investment. This leads to cases where offspring receives more care from a single parent, than the cumulative care of two parents [14]. Offspring that receives more care, may have a better change of survival. For example, more food leads to stronger individuals who are better at fighting off predators and attract more potential mates. This means that the gain from raising offspring alone is not necessarily smaller than the gain of raising offspring together.

## 7.1 Future Work

The inclusion of a spatial dimension is just one extension to the original Battle of the Sexes. Other extensions have been mentioned and in some cases these could be combined to form a more realistic model. Instead of using a regular grid it would be more realistic to use a random grid. This allows players to have a different number of possible mates (and competitors). This could lead to an advantage for one of the strategies where the destiny of potential mates is higher.

The drawback of extensions to the original model is that they make the model more specific and less applicable to more species. The framework by Simão & Todd which tries to incorporate more realism models mate selection in humans. Though the model can still hold for other species, the assumptions made may prevent the model to be applicable to other species where coyness exists. There is a trade-off between models that are widely applicable and models that are more realistic.

The inclusion of a spatial dimension is an option that should be considered when modelling evolutionary games. It has been shown that the spatial dimension influences Hawks vs. Doves, Prisoner's Dilemma, Coordination Games and the Ultimatum Game. The Battle of the Sexes can be added to this list.

# Conclusion

Work by Dawkins and others has shown that in a game theoretical model of the Battle of the Sexes a coy female strategy can survive under certain conditions. In this model there is an equilibrium of mixed strategies. The actual ratio of strategies is predicted to oscillate around this equilibrium point. This can be illustrated with a set of ordinary differential equations that describe the system.

A spatial dimension can be added to the game by modelling a population with a cellular automaton. When the game is played in this spatial manner, one of the two strategies for each sex is driven to extinction and other becomes the dominant strategy in the population. This final population can be easily invaded if one player switches strategies, which means that the dominant strategies are not an ESS and the outcome of the game is not an evolutionary stable state. In a cellular automaton model where stochastic mutations are allowed to occur no strategy will go extinct. Instead the ratio of strategies oscillates around a fixed point, similar to the oscillations predicted by Dawkins. The location of this point is different from the equilibrium by Dawkins and depends on the rate of mutations in the population. This mutation rate also influences the amplitude of the oscillations. This amplitude is also highly influenced by the size of the population.

The result of the a simulation with the cellular automaton with stochastic mutations does not depend on the initial ratio of strategies whereas in the ODE system that describes the system, the amplitude of the oscillations is determined by the initial values. This means that the ODE system can show that a mixed strategy is evolutionary stable,

but not how it evolved to this mixed strategy. The cellular automaton with stochastic mutations can illustrate how mutations can cause a population of pure strategies to evolve into a population of mixed strategies. This corresponds to an evolutionary scenario in nature where a favourable mutation can start off small and result in a population of mixed strategies. The spatial model is also more robust than an ODE system. An ODE system will not recover from a small disturbance, while the spatial model can.

Computationally an ODE model may be more favourable than the simulation of a population since it does not depend on population size. However, populations studied in nature will often be much smaller than 250 000 individuals simulated with a  $500 \times 500$  population, which runs sufficiently fast on any modern computer.

The spatial model confirms that the strategy of female coyness can only survive if unhelpful males are present in the population. For species where the survival of the offspring highly depends on the helpfulness of males, the strategies of helpful males and fast females are an evolutionary stable strategy. This has been shown by other models and it is confirmed by results of the spatial model.

The cellular automaton model can show the influence of mutations on the equilibrium. In general, in the cellular automaton model it is easier to include extensions compared to the PDE model. This includes extensions such as inclusion of new strategies or memory of past events.

---

---

## Bibliography

- [1] R. Alonso-Sanz, *Self-organization in the spatial battle of the sexes with probabilistic updating*, *Physica A*, 390 (2011), pp. 2956–2967.
- [2] M. Bastock, *Courtship: An Ethological Study*, Aldine Publishing Company, 1967.
- [3] P. Battigalli and M. Dufwenberg, *Dynamic Psychological Games*, *Journal of Economic Theory*, 144 (2009), pp. 1–35.
- [4] H. S. Bierman and L. Fernandez, *Game Theory with economic applications*, Addison-Wesley, 1998.
- [5] A. M. Colman, *Game Theory and its Applications in the Social and Biological Sciences*, Butterworth-Heinemann, 1995.
- [6] C. Darwin, *On the Origin of Species*, John Murray, 1859.
- [7] ———, *The Descent of Man, and Selection in Relation to Sex*, John Murray, 1871.
- [8] R. Dawkins, *The Selfish Gene*, Oxford University Press, 1976.
- [9] R. Dawkins and Carlisle, *Parental investment, mate desertion and a fallacy*, *Nature*, 262 (1976), pp. 131–132.
- [10] R. A. Fisher, *The Genetical Theory of Natural Selection*, Clarendon Press, 1930.
- [11] M. Gardner, *Mathematical Games – The fantastic combinations of John Conway’s new solitaire game “Life”*, *Scientific American*, 223 (1970), pp. 120–123.

- [12] J. Geanakoplos, D. Pearce, and E. Stacchetti, *Psychological Games and Sequential Rationality*, *Games & Economic Behaviour*, 1 (1989), pp. 60–79.
- [13] R. Gibbons, *Game theory for applied economists*, Princeton University Press, 1992.
- [14] M. Griggio and A. Pilastro, *Sexual conflict over parental care in a species with female and male brood desertion*, *Animal Behaviour*, 74 (2007), pp. 779–785.
- [15] T. Killingback and M. Doebeli, *Spatial Evolutionary Game Theory: Hawks and Doves Revisited*, *Proceedings: Biological Sciences*, 263 (1996), pp. 1135–1144.
- [16] J. Maynard Smith, *On Evolution*, Edinburgh University Press, 1972.
- [17] —, *Evolution and the Theory of Games*, Cambridge University Press, 1982.
- [18] J. Maynard Smith and G. R. Price, *The Logic of Animal Conflict*, *Nature*, 246 (1973), pp. 15–18.
- [19] J. M. McNamara, L. Fromhage, Z. Barta, and A. I. Houston, *The optimal coyness game*, *Proceedings of the Royal Society B*, 276 (2009), pp. 953–960.
- [20] J. D. Morrow, *Game Theory for Political Scientists*, Princeton University Press, 1994.
- [21] S. D. Mylius, *What Pair Formation Can Do to the Battle of the Sexes: Towards More Realistic Game Dynamics*, *Journal of Theoretical Biology*, 197 (1999), pp. 469–485.
- [22] J. F. Nash, *Equilibrium Points in N-Person Games*, *Proceedings of the National Academy of Sciences of the United States of America*, 36 (1950), pp. 48–49.
- [23] —, *Non-Cooperative Games*, *Annals of Mathematics*, 54 (1951), pp. 286–295.
- [24] J. v. Neumann, *Zur Theorie der Gesellschaftsspiele*, *Mathematische Annalen*, 100 (1928), pp. 295–320.

- [25] J. v. Neumann and O. Morgenstern, *Theory of Games and Economic Behavior*, Princeton University Press, 1944.
- [26] M. A. Nowak, S. Bonhoeffer, and R. M. May, *More Spatial Games*, *International Journal of Bifurcation and Chaos*, 4 (1994), pp. 33–56.
- [27] —, *Spatial games and the maintenance of cooperation*, *Proceedings of the National Academy of Sciences of the United States of America*, 91 (1994), pp. 4877–4881.
- [28] M. A. Nowak and R. M. May, *Evolutionary games and spatial chaos*, *Nature*, 359 (1992), pp. 1507–829.
- [29] —, *The Spatial Dilemmas Of Evolution*, *International Journal of Bifurcation and Chaos*, 3 (1993), pp. 35–78.
- [30] K. M. Page, M. A. Nowak, and K. Sigmund, *The spatial ultimatum game*, *Proceedings of the Royal Society*, 267, pp. 2177–2182.
- [31] P. Schuster and K. Sigmund, *Coyness, Philandering and Stable Strategies*, *Animal Behaviour*, 29 (1981), pp. 186–192.
- [32] U. Schwalbe and P. Walker, *Zermelo and the Early History of Game Theory*, *Games and Economic Behavior*, 34 (2001), pp. 123–137.
- [33] R. Selten, *Reexamination of the Perfectness Concept for Equilibrium Points in Extensive Games*, *International Journal of Game Theory*, 4, pp. 25–55.
- [34] —, *A note on evolutionarily stable strategies in asymmetric animal conflicts*, *Journal of Theoretical Biology*, 84 (1980), pp. 93–101.
- [35] J. Simão and P. M. Todd, *Modeling Mate Choice in Monogamous Mating Systems with Courtship*, *Adaptive Behaviour*, 10 (2002), pp. 113–136.
- [36] P. D. Taylor and L. B. Jonker, *Evolutionarily Stable Strategies and Game Dynamics*, *Mathematical Biosciences*, 40 (1978), pp. 145–156.
- [37] R. L. Trivers, *Parental Investment and Sexual Selection*, *Sexual selection and the descent of man*, 12 (1972), pp. 136–179.

- [38] C.-A. Wachtmeister and M. Enquist, *The evolution of female coyness - trading time for information*, *Ethology*, 105 (1999), pp. 983–992.
- [39] E. F. F. Zermelo, *Über eine Anwendung der Mengenlehre auf die Theorie des Schachspiels*, *Proceedings of the Fifth International Congress of Mathematicians (Cambridge 1912)*, 2 (1913), pp. 501–504.

# Equilibrium Derivation

In *The Selfish Gene* [8] Dawkins shows an example of the Battle of the Sexes. In this model males are strictly helpful or unhelpful and females are strictly coy or fast. Coy females require a male to invest in the relationship before mating by forcing them into an engagement period. Unhelpful males leave if a female refuses to mate immediately and if she does want to mate he leaves directly afterwards leaving the female to care for the offspring alone. A helpful male will share the care over their offspring with a female. Fast females mate immediately, without an engagement period.

Dawkins shows that in some cases both male strategies (helpful and unhelpful) and both female strategies (coy and fast) coexist. This is done by assigning values to the benefit of having offspring, the cost of raising offspring and the cost of an engagement period. Since it is very hard to find a concrete unit to measure the benefit and cost, the example uses arbitrary units. The gain of having offspring is 15, the cost of upbringing is 20 and the engagement period has a cost of 3.

These values allow us to calculate the overall benefit of an interaction between a male and a female. Suppose a helpful male and a coy female meet. First, both invest 3 units in the engagement period. After this, they mate and raise their offspring together. The cost of upbringing is shared, thus they both invest 10 units in raising their offspring. Each of them gains the benefit of having offspring, 15 units. In total, the benefit for both parents is  $15 - 10 - 3 = 2$ .

These values can be worked out for each pair of strategies. Here,  $H$  is used for a helpful male,  $U$  for an unhelpful male,  $C$  for a coy female,

	Coy	Fast
Helpful	(2, 2)	(5, 5)
Unhelpful	(0, 0)	(15, -5)

Table A.1: Payoff matrix for the Battle of the Sexes.

and  $F$  for a fast female. The full payoff matrix is given in table A.1.

Interactions with different strategies have different payoff. This means that if we want to calculate the expected benefit of an arbitrary interaction we need to account for the probability that a player encounters a particular strategy. This will be denoted with  $p(A)$  for the probability of meeting a partner that plays strategy  $A$ .

The expected payoff  $P$  per interaction for each strategy can be written as a function of these probabilities:

$$\begin{aligned} P(H) &= p(C)E(H, C) + p(F)E(H, F) \\ &= 2p(C) + 5p(F) \end{aligned}$$

$$\begin{aligned} P(U) &= p(C)E(U, C) + p(F)E(U, F) \\ &= 15p(F) \end{aligned}$$

$$\begin{aligned} P(C) &= p(H)E(C, H) + p(U)E(C, U) \\ &= 2p(H) \end{aligned}$$

$$\begin{aligned} P(F) &= p(H)E(F, H) + p(U)E(F, U) \\ &= 5p(H) - 5p(U) \end{aligned}$$

From these equations equilibria can be derived. The equilibrium is the point where the payoff for each strategy is equal. If the payoff for all strategies is equal no one can improve their benefit by changing strategies.

$$\begin{aligned} P(H) &= P(U) \\ 2p(C) + 5p(F) &= 15p(F) \\ 2p(C) &= 10p(F) \end{aligned}$$

which is satisfied by  $p(C) = \frac{5}{6}$  and  $p(F) = \frac{1}{6}$ . And:

$$\begin{aligned}P(C) &= P(F) \\2p(H) &= 5p(H) - 5p(U) \\3p(H) &= 5p(U)\end{aligned}$$

which is satisfied by  $p(H) = \frac{5}{8}$  and  $p(U) = \frac{3}{8}$ .

This shows that for the given values the system is in equilibrium if females are coy in  $\frac{5}{6}$  of the interactions and males are helpful in  $\frac{5}{8}$  of the interactions. This does not necessarily mean that  $\frac{5}{6}$  of females should always be coy and  $\frac{1}{6}$  of the females should always be fast. A female that has a mixed strategy of being coy in  $\frac{5}{6}$  of her interactions and fast in the rest of her interactions is also at the equilibrium. The equilibrium only holds for the entire population not necessarily for individuals in that population.



---

---

## Coordination between the Sexes

In game theory, the Battle of the Sexes sometimes refers to a different game than in evolutionary biology [17]. To avoid confusion, in the context of this thesis the term Battle of the Sexes refers strictly to the game of conflict between parents over parental investment. The other game that carries the title Battle of the Sexes will be referred to as *Coordination between the Sexes* (CbtS).

Coordination between the Sexes is a game where two players need to coordinate their actions but have different interest. This asymmetry in interests makes the game an asymmetric game. The classical illustration of the game is a couple that wants to go a date together. The man would prefer to go to a football game and the woman prefers the opera. If they have not agreed on where to go and they can not communicate, where should each of them go? The man might go to the stadium in the hope that the woman shows up there. However, if she decides to go to the theatre it would be better to go there. Attending the opera together is better than sitting in the football stadium alone.

	Football	Opera
Football	(2, 1)	(0, 0)
Opera	(0, 0)	(1, 2)

Table B.1: Payoff matrix for Coordination between the Sexes. The first value denotes the payoff for the male, the second value denotes the payoff for the female.

	Left	Right
Up	$(a_1, a_2)$	$(c_1, c_2)$
Down	$(b_1, b_2)$	$(d_1, d_2)$

Table B.2: The payoff matrix for a coordination game, where  $a_1 > b_1$ ,  $d_1 > c_1$ ,  $a_2 > c_2$  and  $d_2 > b_2$  should hold.

For this game a payoff matrix can be constructed (table B.1). If both go to a different location, both gain nothing. If one goes to the location of their choice with their partner the benefit is 2. If one goes to the location of their partner's choice with their partner the benefit is 1.

As with the Battle of the Sexes, the expected gain of a player depends on the ratio of strategies amongst the other sex. For this game there are three Nash equilibria. If all players always go to the opera, any player that adopts a different strategy is worse off. If all players always go to the football game, any player that adopts a different strategy is also off worse. These strategies are pure. There is also a mixed strategy that is a Nash equilibrium. If a man goes to the stadium in two out of three cases and the woman goes to the stadium in one out of three cases, changing the strategy means your expected gain will be lower.

Coordination between the Sexes is a special case of the coordination game. To compare games it is useful to use the extensive form of a game, which was introduced by von Neumann [24]. The payoff matrix of a coordination game is given in table B.2. The inequalities of a coordination game do not hold for the Battle of the Sexes (e.g. table 4.1). This shows that the Battle of the Sexes is indeed a different game than Coordination between the Sexes.



